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The Monarch Butterfly: A Review

Harrington Wells¹ and Patrick H. Wells²

¹*Faculty of Biological Science, The University of Tulsa,
Tulsa, Oklahoma 74104*

²*Department of Biology, Occidental College,
Los Angeles, California 90041*

Abstract.—A novel view of the monarch butterfly's (*Danaus plexippus*) life history is presented through the synthesis of theories developed in the last few years with more traditional ecological models of the monarch. The important factors directing monarch butterfly population dynamics are now understood to be: 1) Oviposition and Range Dynamics, 2) Energetics, 3) Mating Kinetics, and 4) Predation Deterrence. An understanding of the evolutionary basics and interaction of these factors in *D. plexippus* provides a foundation for the study of other endangered species.

Danaus plexippus, the monarch butterfly, has long been of scientific interest, due to its annual cyclic appearances, spectacular aggregations, and apostatic coloration (Urquhart 1960; Ackery and Vane-Wright 1984; Malcolm and Zalucki 1992). More recently, California monarch butterfly populations have been the center of social-political activity as land development interests in California infringe upon monarch natural habitat (e. g., Schultz 1989; Associated Press 1990; Allen and Snow 1991, Brower and Malcolm 1991). However, only recently has research elucidated several of the factors which drive the unique life history of the monarch butterfly. These selective forces, though more pronounced in *D. plexippus*, present insights for understanding the life histories of a wide range of species, and should be the focus of study in conservation efforts and legal decisions involving monarch butterflies. Although this article is centered on our knowledge of the California populations of *D. plexippus*, the principles should be applicable to monarch butterfly populations worldwide; and in fact, some information utilized for this synthesis is based on non-California monarch studies.

The factors which have interacted to shape monarch life history through natural selection now appear to be: 1) Oviposition and Range Dynamics, 2) Energetics, 3) Mating Kinetics, and 4) Predation Deterrence.

I. Oviposition and Range Dynamics

Oviposition constraint was the first factor recognized as one of the fundamental forces directing the life history of *D. plexippus*. Field observations and laboratory studies indicate that monarch butterflies worldwide oviposit only on plants in select genera of the families Asclepiadaceae (milkweed) and Apocynaceae (dogbane), and that these plants are the only hosts for the larvae (Nicholson 1935; Urquhart 1960; Wise 1963; D'Abrera 1971; Brower et al. 1972; Common and Waterhouse 1972; Tietz 1972; Smithers 1973; Brower 1977; Koch et al. 1977; Ackery and Vane-Wright 1984). Although select Apocynaceae are generally con-

sidered to be monarch host plants, one controlled study claims otherwise (Borkin 1991). Reports of monarch oviposition and larval feeding on plants of additional families (Convolvulaceae, Euphorbiaceae, Malvaceae, Rutaceae) represent rare instances and in most cases are considered questionable (Ackery and Vane-Wright 1984).

Orientation to host plants is probably based initially upon olfaction. Monarch adults typically approach milkweed patches from downwind using a zig-zag behavior characteristic of anemotactic odor search by flying insects (Kennedy 1983; Carde 1984; Wenner and Wells 1990). The ability of *D. plexippus* to find very isolated milkweed patches in coniferous forests (Shapiro 1981) supports this hypothesis. Subsequent host plant recognition by adults appears to be aided by vision and confirmed by tactile chemoreceptors (Urquhart 1960). Apparently, larvae will not feed on plants of other genera even in the absence of these host plants. It is inferred (Ackery and Vane-Wright 1984), and our experience confirms, that California monarch oviposition and larval feeding are as restricted.

Oviposition of eggs invariably occurs on a suitable host plant. Eggs are ovoid, leathery, about 1 mm in length, and appear faceted due to crossing of approximately two dozen vertical with many transverse ridges (Doherty 1886, 1891; Urquhart 1960). Time from laying to egg hatching varies with ambient temperature; it averages 3 to 4 days at summer temperatures ($\approx 30^{\circ}\text{C}$), but takes 8 to 12 days at 18°C (Urquhart 1960). We observed that in Southern California milkweed populations, *D. plexippus* eggs typically hatched 5 to 6 days after oviposition. Eggs are initially cream colored, but change to gray with embryo development (Urquhart 1960).

Larvae escape the egg shell by enlarging an initial transverse slit in the membrane. Upon hatching, the larvae consume most of the egg shell (Urquhart 1960). The larvae feed on host plant tissues while progressing through five instars, each instar having distinct markings, but apparently only statistically separable by size (Urquhart 1960). *Danaus plexippus* larval stage development is temperature dependent. Progression through the five instars (hatching to pupation) requires 10 days at 35°C (Urquhart 1960), but can take as long as 38 days in a cool (7°C) climate (Zalucki 1980, 1982). Basking reduces larval stage duration by as much as 50 percent (Rawlins and Lederhouse 1981). First instar larvae are approximately 2 mm while fifth instar larvae reach up to 50 mm in length. During development of the larvae wet mass increases approximately 1000 fold (Urquhart 1960). Later instars are capable of moving from one host plant to another (personal observations). In general, feeding larvae are negatively geotactic and positively phototactic (Mayer and Soule 1906). Caterpillar markings apparently are aposematic (Ackery and Vane-Wright 1984), and cardenolides consumed from the host plant may act as a predation deterrent (see section IV). When mildly disturbed, larvae wave their tubercles, which has been inferred to be a behavior that deters parasitism (Ordish 1975). Stronger mechanical stimuli cause the larvae to curl and fall to the ground (Urquhart 1960; Ordish 1975), and can also induce oral regurgitation (Brower 1984). Larvae usually wander from the host plant to pupate (Ackery and Vane-Wright 1984).

Pupa formation is initiated by the larva spinning a pad of silk attached to a suitable site from which the pupa can hang. The larva subsequently grasps the silk stalk with its anal claspers and hangs head down, assuming a fish hook shape. Finally, the larva molts and the pupa attaches to the silk pad by means of the



Fig. 1. North American monarch butterfly winter and summer geographic ranges. Overwintering areas are primarily limited to coastal California between San Francisco and Los Angeles, and a small region in the Transvolcanic Mountain Range of central Mexico (striped). Small relicts of summer populations survive in southern Florida and the low deserts of Arizona in some years, but represent insignificant numbers in terms of the population biology of the monarch butterfly. Each spring the geographic range expands from the overwintering areas as depicted by the stippled bands. Monarch populations normally decline in the gulf states in mid summer. Range contraction occurs each fall.

cremaster (Urquhart 1960, 1970). Eclosion occurs 9 to 15 days after pupation, depending upon temperature and other environmental conditions (Urquhart 1960; Petersen 1964a). Pupae are green except for a row of gold spots, whose function remains speculative (Taylor 1964; Petersen 1964a; Urquhart 1960, 1972a, b, c, d, 1973; Ackery and Vane-Wright 1984). Imago emergence from the pupa is described in detail by Urquhart (1960).

Danaus plexippus in California appear to be limited to plants of the genus *Asclepias* plus *Apocynum androsaemifolium* (taxonomy of Munz and Keck 1970). *Asclepias* are perennial herbs, which under normal west coast conditions, annually die back to their deep-seated roots. West coast milkweeds reappear each spring (primarily from underground rootstock), first in California southern coastal regions, followed by *Asclepias* populations at progressively higher elevations and more northerly latitudes (Munz and Keck 1970). Monarch butterflies are sequentially abundant at these seasonal oviposition sites (Urquhart 1966). The result is a displacement of the population annually, with the population center following a geographically cyclic pattern each year (Williams 1958; Urquhart 1960; Johnson 1969; Orr 1970; Nagano et al. 1992) as depicted in Figure 1.

A similar pattern of geographic range expansion moves annually from central Mexico towards southern Canada east of the Rocky Mountains (Urquhart 1976; Urquhart and Urquhart 1976b; Brower 1977), and in parts of Australia (Smithers 1965, 1977, 1983). Studies based upon Mexican monarchs show that butterflies

at the extremes of their summer geographic range are several generations distant from the individuals leaving the overwinter areas (Brower 1961; Herman 1988). Presumably the same is true for California based populations. Therefore, several generations annually are required to complete the geographic cycle.

Physiologically, none of the developmental stages of the monarch butterfly can survive prolonged freezing temperatures (Zalucki 1982; Ackery and Vane-Wright 1984). Range contraction to frost free zones in the winter, therefore, correlates both with survival and the region where hosts plants will first reappear. The wintering areas in California are typically frost free, support vegetation for roosting, and offer moisture sources. They are also cool throughout the night and during most hours of the day (Hill et al. 1976; Tuskes and Brower 1978; Chaplin and Wells 1982). The monarch's behavior of moving to warmer microhabitats within the overwinter areas provides further assurance of survival from occasional frosts (Calvert et al. 1983; Calvert and Cohen 1983). Suitable vegetation helps to provide a frost free environment, and is thus one important aspect of overwintering areas (Calvert and Brower 1981).

The winter geographic range of *D. plexippus* in California is, in fact, not only limited mainly to coastal regions between San Francisco and Los Angeles but is also centered in a small number of large aggregations within that coastal area (Williams et al. 1942; Urquhart 1960; Urquhart et al. 1965; Wenner and Harris 1991). These large overwinter aggregations are each composed of between 50,000 and several hundred thousand butterflies in California, to perhaps several million butterflies at some sites in Mexico. Aggregations coalesce in late fall. Butterflies roost in groups upon trees in the aggregations. Except for occasional flights to drink water there is little activity throughout winter in these large clusters (Fig. 7, 8). Without water, however, mortality due to desiccation occurs in overwintering butterflies. Thermoregulation by shivering, movement to warmer microhabitats, and basking are important, since these behaviors allow butterflies to attain body temperatures at which flight to obtain water is possible on cool days (Krammer 1970; Masters et al. 1988).

Smaller fall clusters which coalesce in the coastal region apparently are of a more transient nature, existing only until temperatures decline (Ackery and Vane-Wright 1984; Nagano et al. 1992). Members of these transient clusters may gradually join the major overwinter aggregations as winter progresses. However, it is also possible that mortality is high for butterflies in transient clusters and that most individuals do not survive winter. Additional continuously breeding winter populations in coastal California south of Los Angeles have been mentioned in mark and recapture studies focused upon the Los Angeles basin (Urquhart et al. 1970). Study of these populations over an entire winter, however, is likely to show that few butterflies actually survive. Native milkweeds of this region die back to rootstock in winter, and there is a dearth of food resources for nectivores. Only unnatural conditions created by suburb expansion would create exceptions.

Finally, a few West Coast monarchs, at least theoretically, may overwinter in the Arizona-California low deserts; e.g., Funk (1968) reported such an observation for southwestern Arizona. At present, the regularity of overwinter low desert monarch populations is doubtful, and occasional monarch butterflies in this region during winter are probably insignificant in the overall natural history of the species.

Sustained periods of flight, thought by some to be involved in range contraction, may lead to juvenile hormone inactivation (Lessman and Herman 1981), and

this in turn degrades maturity of both male and female reproductive tracts (Herman 1975a, b; Herman et al. 1981). However, low post-eclosion temperature appears to be the primary environmental factor which leads to reproductive dormancy in both sexes of monarch butterflies (Barker and Herman 1976; James 1983). Photoperiod apparently does not control reproductive tract maturity (James 1983), but it may be a factor influencing reproductive behavior (Barker and Herman 1976). Photonegative behavior of overwintering butterflies may indirectly curtail reproductive tract development by minimizing heliothermic warming (James 1983).

During overwinter aggregation, reproductive tract maturity of most monarch butterflies is not complete (Herman et al. 1989), and mating is rare (Hill et al. 1976; Tuskes and Brower 1978); however, oligopause is incomplete in California populations (Ackery and Vane-Wright 1984). A similar natural history has been described for monarchs in southeastern Australia (Smithers 1965; James 1979), including absence of a true reproductive diapause (James 1982; James and Hales 1983), and in central Mexico (Urquhart 1976; Urquhart and Urquhart 1976b; Brower et al. 1977), where oligopause (possibly true diapause: Herman 1981) can be complete and of a longer duration (Herman et al. 1989).

Alternative theories have been proposed to account for fall contraction of the range of *D. plexippus*. The long distance directed (LDD) migration hypothesis infers that California overwintering populations are the product of a fall adult monarch flight from southwestern Canada, Washington, Oregon, and northern California (Urquhart and Urquhart 1977) down the coast, and from the western slopes of the Rocky Mountains and Sierra Nevada Mountains through the Sacramento and San Joaquin Valleys to coastal regions of California (Urquhart and Urquhart 1977). The summer range of *D. plexippus*, under the LDD migration hypothesis, is geographically density skewed, such that the highest densities of monarch butterflies occur in regions farthest from the overwinter areas (Urquhart 1966). Eastern monarch populations, originating from Mexican overwinter sites, do in fact decline (are often absent) in mid-summer throughout the Gulf Coast states and are largest in states bordering Canada (Brower 1961, 1962; Neck 1976; Urquhart and Urquhart 1976a), due perhaps to monarch intolerance of high temperatures (Malcolm et al. 1987). According to the LDD migration hypothesis, individuals leaving the summer range are the same individuals as those that arrive at the overwinter sites; the seasonal movement is thought to resemble that of migratory birds (Urquhart 1960).

Alternatively, the California overwinter population of monarch butterflies has been hypothesized to reflect a relatively local range contraction; most individuals of the more extreme summer range simply die as winter weather comes to the areas they inhabit (Smithers 1977; Wenner and Harris 1992). Overwintering California aggregations have been predicted under this theory to be primarily the result of autumn upwind flight by butterflies produced in summer populations (Wenner and Harris 1991) of the Sacramento and San Joaquin Valleys, adjacent lower and mid-elevation Sierra Nevada and coastal mountains (Ackery and Vane-Wright 1984), as well as the coastal plain and river drainages (Wenner and Harris 1991).

Thus, the large overwinter aggregations are thought by some to be the direct result of long distance directional migration to avoid harsh northern winters (Urquhart 1960). Others believe these aggregations are the result of seasonal

contraction of the environmentally suitable monarch butterfly range, thus representing relatively local surviving individuals (Wenner and Harris 1992). Note, however, that neither the migration nor the seasonal range contraction hypothesis explains winter monarch aggregation; dispersed roosting in the overwintering regions would be as beneficial under either of these theories.

Lipid content of monarch butterflies arriving at the overwinter range is high, as would be expected under the local range constriction hypothesis (Chaplin and Wells 1982). However, a version of the LDD migration theory suggests that feeding during migration might produce similar results (Brown and Chippendale 1974), especially given the speculation that flight-work may be minimized by soaring flight behavior (Gibo and Pallet 1979; Gibo 1981). Future determination of summer range geographic density distribution may help to resolve the debate. That is, data may show any LDD migratory individuals to be an unimportant percentage of the California overwinter population, particularly if probability of death due to random misfortune is related to distance traveled. On the other hand, density distribution may indicate that there is not locally a large enough population to represent an important fraction of the overwinter aggregations, although this argument seems untenable for Santa Barbara County (Wenner and Harris 1992).

Aggregations also have been theorized to be sanctuaries where, *en masse*, individuals are protected by metabolic heat and thermal insulation from winter cold. However, studies designed to test this hypothesis did not find a temperature gradient between the outside and center of overwintering groups of butterflies (Chaplin and Wells 1982), as found in some communal bees, and isopods (Simpson 1961; Friedlander 1965; Wilson 1971).

Three additional lines of evidence also suggest that aggregations are not the result of selection by this environmental factor. First, aggregations in California have remained coastal, and Mexican populations inland. Selection would be expected to have either caused Californian overwintering aggregations to move to cooler elevations, where metabolic rates would be lower, or Mexican overwintering clusters to move to lower elevations where the likelihood of death due to freezing would be minimized.

Second, new aggregation site formation can occur, as evidenced by monarch clusters in *Eucalyptus* forests in California (e.g., Urquhart et al. 1965; Hill et al. 1976). *Eucalyptus* species were introduced, the *Eucalyptus* forests subsequently planted, and their use as roosting sites established within the last 150 years (Chaplin and Wells 1982). Thus, locations of Californian and Mexican aggregation sites cannot be ascribed to innate behavior which inhibits selection for new cluster localities.

Finally, if clustering were simply the result of a selection which would protect butterflies from occasional freeze periods, California coastal populations would be largely exempt from selective pressure to aggregate. Aggregation within the winter range of the monarch is thus not explained simply by distribution of oviposition sites or geographic areas which are equable throughout winter.

II. Energetics

The second major factor shaping the life history of the monarch butterfly is energetics. Energetics, the dynamics of metabolism and the processes whereby energy is stored chemically is, of course, basic to all life. Just how energetics has

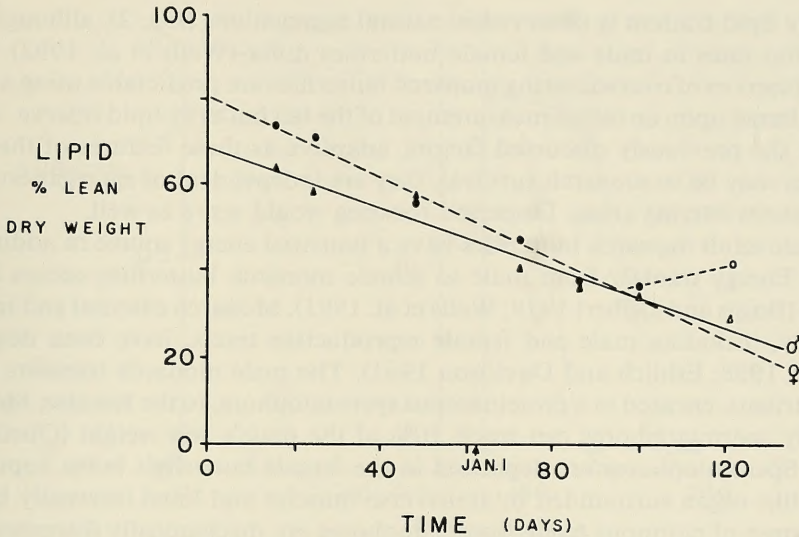


Fig. 2. Least squares linear regression performed separately on male and female data. Each point represents 25 pooled individuals (all male or all female). Regression analyses were performed on pre-mating samples (solid points). Male and female regressions are significantly different. Only the female post-mating sample (o, male Δ) was significantly different than predicted by the 95% prediction limits based on the regression analyses (from Wells et al. 1992).

shaped the life history of *D. plexippus*, however, has only gradually become apparent over the past ten years.

Winter presents the monarch butterfly with acute energetics problems not normally faced by most species. Specifically, energy resources for both monarch adults (nectar) and larvae (milkweed) are scarce or absent during winter throughout the West Coast geographic range of *D. plexippus* (Tuskes and Brower 1978; Chaplin and Wells 1982). The scant nectar resources that may be present (Brower 1977) are insignificant in terms of monarch energetics (Ackery and Vane-Wright 1984). Similar conditions exist seasonally for Mexican and Australian aggregating monarchs (James 1984; Masters et al. 1988). Monarch butterflies must overwinter on stored lipid reserves (Chaplin and Wells 1982; James 1984; Masters et al. 1988).

Particularly important in this light is the fact that metabolic rates of ectotherms are dependent upon temperature of the environment; ectotherm metabolism exponentially increases as temperature is raised (Gordon 1968). This correlation dictates that the overwinter range of the monarch butterfly must be consistently cool. Otherwise, death from starvation would occur prior to the availability of spring oviposition sites (Chaplin and Wells 1982).

Even though North American *D. plexippus* is very widely distributed throughout summer, the physiological limits requiring above freezing temperatures and the energetics requirement of a continuously cool climate severely constrict the winter range of the monarch butterfly (Calvert and Brower 1985). California south coastal areas are the only predictably cool frost-free winter regions with moisture sources west of the Sierra Nevada. Under these conditions lipid reserves of inactive butterflies within the winter cluster should not be rapidly depleted by basal metabolic processes (Chaplin and Wells 1982). In fact, a slow and linear decline in

butterfly lipid content is observed in natural aggregations (Fig. 2), although lipid utilization rates in male and female butterflies differ (Wells et al. 1992). Thus, energy reserves of overwintering monarch butterflies are predictable using a linear model, based upon an initial measurement of the fall butterfly lipid reserve. Again, as with the previously discussed factors, adaptive as these features of the environment may be to monarch survival, they are independent of aggregation *per se* within the wintering areas. Dispersed roosting would serve as well.

Female adult monarch butterflies have a potential energy source in addition to nectar. Energy transfer from male to female monarch butterflies occurs during mating (Boggs and Gilbert 1979; Wells et al. 1991). Monarch external and internal anatomy, including male and female reproductive tracts, have been described (Erhlich 1958; Erhlich and Davidson 1961). The male monarch transfers sperm and nutrients, encased in a proteinaceous spermatophore, to the females. Monarch butterfly spermatophores can reach 10% of the male's wet weight (Oberhauser 1988). Spermatophores are deposited in the female butterfly's bursa copulatrix, a sack-like organ surrounded by transverse muscles and lined internally by four lateral rows of chitinous teeth. Spermatophores are mechanically disrupted open by the bursa copulatrix (Rogers and Wells 1984) and released nutrients are very quickly incorporated into both reproductive and non-reproductive female tissues; incorporation of labeled spermatophore carbon is detectable within four hours (Boggs and Gilbert 1979; Wells et al. 1992). Rapid assimilation suggests that a specialized mechanism for material absorption may have evolved in the female reproductive tract. However, details of the nutrient absorptive process and the molecule or molecules absorbed are still not well defined.

Just prior to and during dispersal of aggregations a "frenzied" period of mating occurs for approximately two weeks. Photoperiod and temperature act together through the neuro-endocrine system, and regulate reproductive activity (Herman 1973). Temperature appears to be the dominant factor determining the rate of egg maturation (Barker and Herman 1976; James 1983). This intense mating period probably is the first coincidence of warm weather and longer days. Individual monarch butterflies mate repeatedly during this mating period (Hill et al. 1976; Tuskes and Brower 1978). However, monarch butterflies mate at most once per day, due to an extensive copulation time (average 10 hrs, Shields and Emmel 1973; Hill et al. 1976; Ackery and Vane-Wright 1984; Oberhauser 1988; 6 to 18 hrs, personal observations). Energy transfer from male to female butterflies through multiple mating has been demonstrated to significantly increase lipid reserves of overwintering female butterflies in natural California aggregations at the time of aggregation dispersal (Wells et al. 1992). In fact, average female lipid content increases approximately 60% during this mating period. Multiple mating is thus critical for significant energy gain by females at this time of year.

Due to the intensive mating period whereby both male and female butterflies mate repeatedly at the time of aggregation dispersal, female energy reserves increase markedly. After the period of intensive mating, female energetics suddenly are no longer represented solely by depletion of fall lipid reserves. Female butterfly energy reserves after aggregation dispersal must include nutrients gained through mating. These two models have been the key to evaluating the effect of multiple mating on fecundity, generating testable expectations, and contributing to our current concept of monarch butterfly life history.

Nectar resources are, in fact, few and not abundant even at the time of aggre-

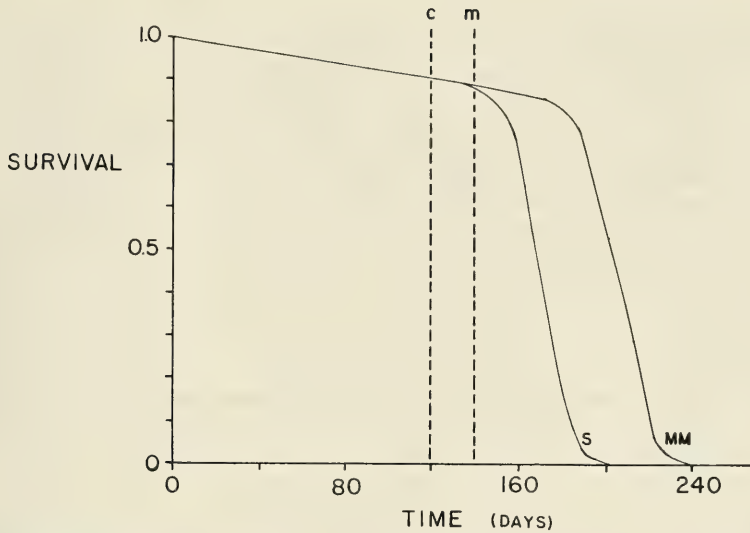


Fig. 3. Mathematical model of female butterfly survival versus time with and without the multiple mating resulting from February mating frenzy. Survival is based on chance death and upon lipid energy reserves which are depleted while overwintering (death due to starvation). Lipid depletion rates and fat content used were those observed (Fig. 1). MM = multiple mating, S = single mating, c = mean time of cluster dispersal, m = mean time of milkweed first appearance (from Wells et al. 1992).

gation dispersal (Tuskes and Brower 1978). The continued energy impoverishment of males during this period confirms that nectar foraging is not a primary source of increased female energy reserves. Successful reproduction requires that females disperse to the locations of species of plants suitable for oviposition. Increased life expectancy at this time relates directly to female oviposition success. Overwintering female fecundity is thus a function of life expectancy after aggregation dispersal (Wells et al. 1992).

Female life expectancy has been modeled by Wells et al. (1991) based upon the probability of escaping death due to random misfortune, and the probability of avoiding death from starvation. Using the linear models described, and the assumptions that both lipid reserves of individual females entering overwinter aggregations and individual female energy gain through mating are normally distributed and independent, evidence exists that time of death due to starvation in the female population is normally distributed. Normal cumulative distribution functions thus describe life expectancy based on energetics with or without multiple mating, given that nectar resources are not available. The only difference is that the mean and variance in life expectancy are increased with multiple mating.

Lipid reserves at the time of aggregation degeneration determine female ability to disperse into the environment (Ackery and Vane-Wright 1984). Female monarch life expectancy based on overwinter metabolic rate is displayed in Fig. 3, with and without energy gained by females through multiple mating. Energy gain through multiple mating is predicted to significantly increase female longevity, and as a result, increase fecundity (Wells et al. 1992). Altered estimates of net lipid metabolic rate in dispersing females would not change the basic conclusion; longevity of females in the two groups would be changed equally. Thus, multiple mating would increase overwinter female butterfly fitness, and would be favored

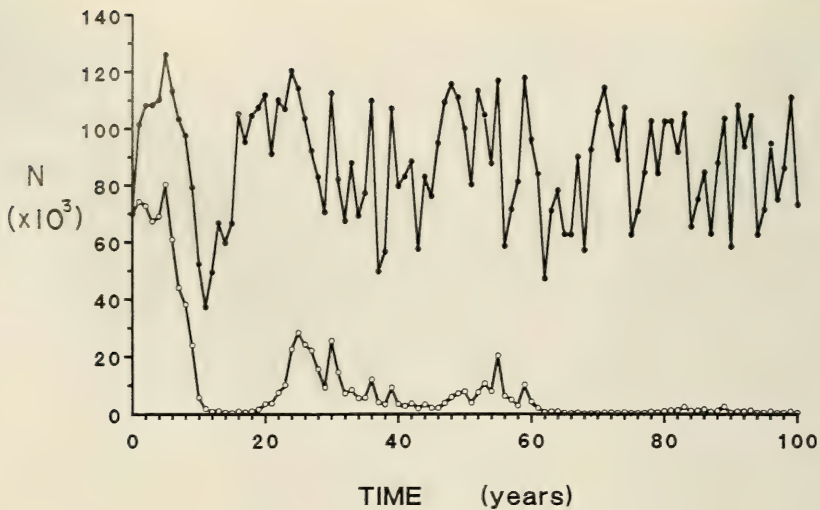


Fig. 4. Monte Carlo simulations of monarch aggregation population size. Number of individuals (N) in an aggregation versus time with multiple mating ($\bullet$) and without multiple mating ($\circ$) are presented. Life expectancies of overwintering monarchs are based on Figure 3. First appearance of milkweed each year ($u = 140$ $\sigma = 10$) and summer population fitness as it relates to population growth rate (e^{m_i} , $u_m = 1$, $\sigma_m = 0.1$) were variables, normally distributed and independent. Summer population growth was based on the Pearl-Verhulst logistic model (Pielou 1977) with carrying capacity 100,000,000 and 5 generations per summer. The probability of last summer generation butterflies reaching the overwinter aggregation is 0.0015. Without multiple mating monarch populations decline to the point where extinction is likely.

by selection in the female population. Under conditions where food is abundant for nectivores, energy transfer from males to females is not an important factor for female survival (Svard and Wiklund 1988); correspondingly, monarchs need not aggregate under these conditions (e.g., Hawaii: Etchegaray and Nishida 1975; N.E. Australia: Smithers 1977).

Studies based on Australian monarch butterflies show that females move from milkweed patch to milkweed patch after dispersal from overwinter aggregations, rather than remaining at a single patch (Zalucki and Kitching 1982, 1984). This behavior leads to discovery of oviposition sites by a female as a linear function of time; thus oviposition rate is a constant. Expected total eggs oviposited by an overwintering female throughout its life is then predictable, based upon milkweed first appearance. When variable time of spring milkweed first appearance is also considered, Monte Carlo simulations using this model of population dynamics have demonstrated (Wells et al. 1992) that, without multiple mating, monarch populations would decline to the point where extinction would be inevitable in poor years (Fig. 4). Energetics are thus a central factor driving the life history of *D. plexippus*.

III. Mating Kinetics

The concept that a third central factor is important in determining the life history of the monarch is only now being realized. This third factor involves the reproduction dynamics of the monarch and may explain why overwintering monarchs are densely aggregated.

Monarch butterflies become active daily in large numbers just prior to aggregation dispersal. Thousands of butterflies are flying simultaneously at that time in the aggregation sites, resulting in a mating frenzy. Male monarch butterflies can be distinguished from females by the presence of a small black spot (alar organ) on each hind wing but that dimorphism is inconspicuous in flight. Females do not appear to actively seek male monarchs. Nor do males expose hairpencils and perform courtship maneuvers (Hill et al. 1976) as has been reported for other danaine butterflies (Ackery and Vane-Wright 1984). Rather, mating occurs through male chase and in-flight capture of females. A male only chases females which by chance come relatively close to it through crossing of flight paths. A male captures a female in-flight by pouncing on her (Hill et al. 1976). The pair tumble to the ground, where the male physically overpowers the female and initiates copulation (Fig. 9, 10, 11). The male subsequently flies, carrying the female to a roosting site where copulation (Fig. 9, 10, 11) continues for several hours (Hill et al. 1976). Similar behavior has been observed in the laboratory (Rothschild 1978) and in summer populations (Zalucki and Kitching 1982; Oberhauser 1988). Rarely, males have been reported to "nudge" a female toward the ground rather than overpower her (Pliske 1975).

Male butterflies do not always chase females when flight paths cross, or always capture chased females. In fact, males do not only chase female monarchs. A male butterfly will sometimes chase another male when they cross flight paths. If a male captures a male, however, the pair separate soon after falling to the ground (Hill et al. 1976). Flying males will sometimes even chase objects, such as falling leaves or tossed sticks, if they come relatively close, and even an occasional "amorous advance" toward a passing bird has been reported (e.g., Slansky 1971; Smith 1984; Winter 1985). Aberrant mating attempts become more prevalent toward the end of the period of intense mating which precedes dispersal, as the ratio of females to males in the aggregation declines (Hill et al. 1976).

Butterflies appear to mate at most once per day, a limit imposed by the extended period of copulation. However, monarchs can only potentially mate if two come physically close enough to detect each others presence; in terms of kinetic theory: "collide." A "collision" between monarchs may be defined as two butterflies coming into close proximity, although no physical contact is implied or need occur (Wells et al. 1990). The collision rate of butterflies is analogous to the collision rate of randomly moving gas molecules in a container because: 1) A male appears to interact with a female monarch butterfly only when they come into relatively close proximity, and both are in-flight; and 2) Butterflies coming into close proximity (a collision) while flying seems to result by chance crossing of flight paths. The rate constant for butterfly collision has therefore been shown to be a function of the squared density of butterflies (Wells et al. 1990).

Monarch butterfly mating frequency thus obeys second order kinetic laws, rather than Malthusian first order kinetics (Malthus 1798). Furthermore, unlike the Pearl-Verhulst or Lotka-Volterra type models (Verhulst 1838; Pearl and Reed 1928; Lotka 1925; Volterra 1931; Pielou 1977), increased density increases rather than slows the rate of increase in the population of mated individuals.

The rate of change of in-flight non-mated males on any specified day has been shown to be equal to that of females. The fraction of the in-flight female, q_t , and male, p_t , butterflies which have not mated by time t on a specified day may thus be predicted by equation (1) when $h = 0$, and by equation (2) when $h \neq 0$; where

$h = X_o - Y_o$, Y_t equals female density (X_t male) at time t on the specified day (Y_o is Y_t at time zero), and "a" is a constant based on rate of mating success of collisions (Wells et al. 1990).

$$q_t = Y_t/Y_o = p_t = X_t/X_o = 1/(aY_o t + 1) \quad (1)$$

$$q_t = Y_t/Y_o = h/[(Y_o + h) e^{ah t} - Y_o]$$

$$p_t = X_t/X_o = h/[(Y_o + h) - Y_o e^{ah t}] \quad (2)$$

Increased density of butterflies, due to second order reproduction kinetics, increases the probability each day that each individual will mate (Fig. 5). Furthermore, high population densities result in most mating occurring in the first few hours of butterfly activity each day regardless of the length of time during which the environment is conducive to activity (Wells et al. 1990). This phenomenon may be crucial to the monarch butterfly's successful reproduction in California overwinter clusters where cool early spring temperatures may allow only a few hours of activity per day. Thus, the length of time during each day in which environmental conditions are conducive to in-flight butterfly activity affects the population densities required for monarch butterfly populations to increase in number, because multiple matings are necessary for successful reproduction. In essence, second order reproduction kinetics interacting with energetics of lipid reserve depletion and energy gain through mating, a variable time for the appearance of oviposition sites, and an environmentally constrained period of daily activity, make very dense aggregations advantageous compared to dispersed or semi-aggregated overwinter roosting.

The cumulative number of matings per individual increases linearly with each day of the spring mating frenzy as long as the daily probabilities of mating for male and female butterflies remain relatively constant. A linear relation exists between frequency of mated females per day and the cumulative number of matings per female (Wells et al. 1990). As percent mated females each day increases, cumulative number of matings per individual increases.

However, since probability of a female mating on a specified day is not linearly related to density, the cumulative number of matings asymptotically approaches the number of days mating could have occurred as cluster density increases (Fig. 6). The number of times an individual has mated thus becomes essentially density independent at high population densities. The same relation exists for male probability of mating each day (Wells et al. 1990). Under these conditions only high density aggregations cause mating success to approach first order kinetics. Therefore, high densities of butterflies are critical for widespread multiple mating in overwinter populations and, in turn, maximum fecundity. This transition in monarch mating dynamics from second to first order kinetics is predicted on theoretical grounds, using data from California monarchs, to become significant in overwintering aggregations of about 50,000 individuals and essentially complete when aggregations reach 200,000 individuals (Wells et al. 1990).

Decreasing density decreases the mating frequency of both males and females each day if the sex ratio remains unchanged. However, since the rate of female emigration exceeds that of males, sex ratio in the aggregation does change (Hill et al. 1976); the net result is an increase in the mating frequency of remaining females even though the population density declines (Wells et al. 1990).

Males are energetically capable of mating 11 or 12 times during the spring mating frenzy (based upon the Wells et al. 1991 model for an average year and

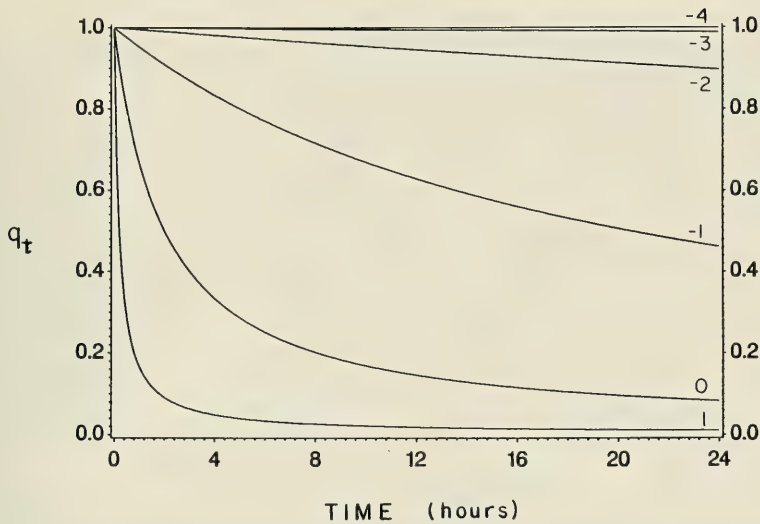


Fig. 5. Effect of functional day length and population density on mating frequency, when frequency of males equals frequency of females in the population ($h = 0$). Frequency of unmated individuals ($q_t = p_t$) versus time during any specified day is depicted (unmated male frequency equals unmated female frequency). Results are given for values of aN_0 from 10^1 to 10^{-4} (curves 1 to -4). Percent unmated individuals asymptotically approaches zero. Higher densities accelerate decline in frequency of unmated individuals (from Wells et al. 1990).

on cumulative mating frequencies observed by Zalucki and Sasuki 1987). Statistically, less than 00.20% (using 11 matings), or 00.01% (using 12 matings), of the males would exceed those limits if it were energetically possible. Thus, male mating behavior in overwinter aggregations does not appear to be significantly influenced by energy limitations.

The model predicts that, at least in overwintering butterflies, egg fertilization dependency on mating order (e.g., first, last, each) would not select for altered male behavior. Prior to the spring mating frenzy, environmental conditions are generally too cool for in-flight activity and mating, although oligopause is not complete. Occasional warm winter days would be too short to substantially increase the rate of gamete maturation, and days would still have a short photoperiod; both would inhibit mating.

After aggregation dispersal, the probability of mating is very low because butterfly density is low and mating success is a second order kinetic function. This is true even if females are still receptive. Finally, during the spring mating frenzy males energetically are capable of mating every day that they can catch a female. Thus, by mating every day a male would maximize its fecundity during the spring mating period (Wells et al. 1990).

In fact, some data now exist which suggest that, in addition to oviposition sites, both energetics and second order reproduction kinetics may even be limiting factors for non-overwintering monarch butterflies. That is, empirical evidence implies that multiple mating is also important energetically to non-overwintering female butterflies (Suzuki and Zalucki 1986; Zalucki and Suzuki 1987; Oberhauser 1988; Zalucki 1992). Furthermore, individual male behavior during location and capture of female monarchs for mating appears to be mechanistically similar in non-overwintering individuals (Zalucki and Kitching 1982; Oberhauser 1988) and

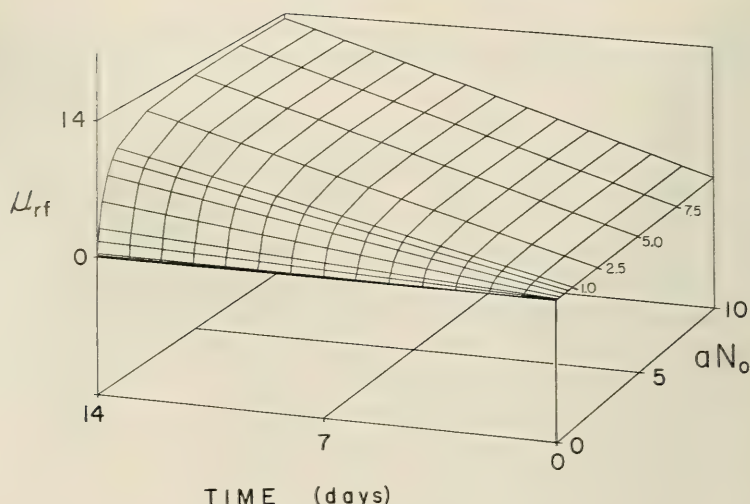


Fig. 6. Mean number of matings per individual (u_{rf}) versus number of days mating frenzy has occurred versus relative population density (aN_0) for $h = 0$. A transition occurs, after which increasing aggregation density has little additional effect on mean number of matings per individual. Essentially, reproduction kinetics change from second order to first order when considering reproduction on a population basis (from Wells et al. 1990).

in laboratory colonies (Rothschild 1978). A conclusion which necessarily follows is that mating frequency in non-overwintering populations should also obey second order kinetics. Population density should be no less a factor in monarch butterfly reproduction dynamics during summer than it is for overwintering populations.

The densities at which reproduction approaches first order kinetics in non-overwintering populations, however, should be reduced from densities required in overwinter aggregations, due to extended daily flight activity, greater food availability, and partially restored lipid reserves. Aggregation, although of a less dense nature, should still be important for efficient reproduction in non-overwintering populations (Wells et al. 1990).

In this light, observations of monarch butterfly clustering about oviposition sites (Zalucki and Kitching 1982, 1984; Bull et al. 1985; Suzuki and Zalucki 1986; Zalucki and Suzuki 1987; Zalucki 1992) are very interesting, since these summer concentrations are predicted theoretically. Male monarchs tend to remain at a milkweed patch, while females move from patch to patch. This behavior maximizes butterfly density at specific localities in the environment, maximizes multiple mating of females, minimizes male energy expenditure, and maximizes distribution of larvae among food resources.

IV. Predation Deterrence

High population densities necessitated by second order kinetics, and the monarch butterfly's relatively large physical size, would be expected to have fostered acute predation problems for *D. plexippus*. Instead, second order reproduction kinetics has led to strong selection for a predation deterrent; one predation deterrent that meets this prediction is cardenolide-based toxicity (Parsons 1965),



Fig. 7. Monarchs drinking water from dew. Although overwintering *D. plexippus* do not require a food source, they need a source of water to survive winter.

combined with apostatic coloration (Brower et al. 1967, 1968; Brower 1969, 1984). The effectiveness of that deterrent, and the importance of predation under some conditions, is attested to by a mimicry complex which includes the resemblance of *Limenitis archippus* to *D. plexippus* (Brower 1958, 1960; Brower et al. 1964; Platt et al. 1971, Ritland and Brower 1991).

The prediction that toxicity, coupled with apostatic coloration, has evolved in concert with the winter aggregation required for successful reproduction is also supported by modeling studies of avian predation on monarch butterflies (Pough et al. 1973). Non-palatability is only an effective predation deterrent when butterflies are densely aggregated (Pough et al. 1973). This prediction has, in fact, been confirmed by predation studies of summer butterfly populations (Petersen 1964b; Waldbauer and Sternburg 1987).

Apostatic coloration combined with monarch toxicity would not be expected to have evolved until monarchs overwintered in aggregations, since evolution of a trait prior to, or independent of, natural selection does not generally occur. Furthermore, while predation models do not predict a maximum density of monarch butterflies in overwinter aggregations, and in fact predict ever greater numbers of individuals in clusters (Calvert et al. 1979), second order kinetics does predict aggregation densities at which ever larger aggregations have no beneficial effect (Wells et al. 1990).

Since toxicity of individual butterflies can vary widely, automimicry is some-



Fig. 8. *Danaus plexippus* overwinter aggregation in California. Monarch aggregations are always in forests, usually around a small clearing and close to a water source. Throughout winter butterflies hang from branches in the aggregation area except for trips to drink water.

times an important aspect of the predation deterrent (Brower and Moffit 1974). Some avian insectivores have learned to taste butterflies for cardiac glycoside content (Brower and Glazier 1975) and have learned in some areas of Mexico to eat only less toxic tissues of functionally less-toxic individuals (Calvert et al. 1979). Predation under these conditions can be substantial (accounting for 75% of butterfly mortality), and is inversely related to aggregation size (Calvert et al. 1979). This type of avian behavior only appears to result in substantial monarch mortality when *D. plexippus* populations contain a relatively high percentage of palatable individuals (Calvert et al. 1979). Predation by mice also appears to be significant under these conditions (Glendinning et al. 1988).

Cardenolide sequestration by monarchs to saturation levels when feeding on *Asclepias* with widely variant cardiac glycoside contents appears to be evolutionarily important (Martin and Lynch 1988; Malcolm and Brower 1989; Malcolm et al. 1989). The fact that highest concentrations of cardenolides are in the wings (Calvert et al. 1979), by which predators capture monarchs (Smith 1979), may also be adaptive. However, cardenolide sequestration to saturation in and by itself does not protect monarch butterflies from predation, as illustrated by Mexican *D. plexippus* which apparently feed largely on species of *Asclepias* with low potency cardenolides (Fink and Brower 1981). Palatability is not only a function of cardiac glycoside concentration, but also the type of cardenolide fed upon by larvae, and the species of avian predator (Fink and Brower 1981).

While occasional beak marks in monarch wings are observed, significant avian



Fig. 9. Male monarch butterfly attempting to mate with a female. The male monarch chases the female, and upon capturing her, the two tumble to the ground where the male attempts to mate with the female. If successful, the male will fly to a branch carrying the female, where copulation will continue for several hours.

and mouse predation on monarch butterflies is not characteristic of California overwintering populations (Brower and Moffit 1974; Calvert et al. 1979). California monarch variability in cardenolide concentration is similar to that observed in Mexican populations. However, the cardenolides found in some California overwintering monarchs are more emetic (Brower and Moffitt 1974; Fink and Brower 1981).

California *Asclepias* species differ in their toxic glycoside contents and there are clonal variations within the species. The narrow leafed *A. fascicularis* is relatively nontoxic, as are approximately 47% of *D. plexippus* in the winter aggregations. Toxicities of *A. californica* and *A. speciosa* are higher, on the order of 0.15 mg cardenolide/g dried plant tissue, while glycoside contents of *A. eriocarpa*, *A. erosa* and *A. vestita* often exceed 1.0 mg/g dried plant tissue (Roeske et al. 1976). Chromatographic profiles of sequestered cardenolides in monarch butterflies raised on specific California milkweeds have also been determined (e.g., Brower et al. 1982, 1984a, b).

Larval densities also pose mortality problems for the monarch butterfly. While predation by vertebrates may be deterred by the chemical defense obtained from the host plant, parasitism by dipterans apparently is not. Tachinid fly parasitism of monarch larvae can kill up to 100 percent of the larvae in a milkweed patch, but parasitism frequencies appear to vary widely between patches (Hill 1973; Etchegaray and Nishida 1975; Zalucki 1981; pers. obs.). Monarch females, by



Fig. 10. Monarch butterflies mating. During an extended copulation time a source of energy is transferred to the female as well as sperm. The energy gained is thought to increase the female butterfly's life expectancy, and hence fecundity.

ovipositing in many milkweed patches, would maximize the frequency of having at least some offspring survive.

V. Perspective

The monarch, *Danaus plexippus*, is an immensely popular butterfly; size, color, distribution, abundance, and conspicuous winter aggregations give the monarch "celebrity status." Biology students are introduced to mimicry theory by the classical monarch-viceroy example (e.g., Curtis and Barnes 1989; Villet et al. 1989; Campbell 1990). Winter roosting, summer breeding, and land use issues involving monarchs are given media coverage (*op. cit.*). The monarch has even been nominated as the United States National Insect (H.J. Res. 411, introduced by Congressman Leon Panetta of Santa Cruz)! This high profile of the monarch butterfly cultivates appreciation of nature, sensitizes the public to ecological issues, and creates a positive image of science.

On the negative side, familiarity may foster complacency, a sense that our knowledge of the monarch butterfly is complete and correct. Familiarity also may encourage concept-centered biology (Wenner 1989) which quashes controversy and narrowly interprets natural history in support of a single popular hypothesis. Either of these simplifications retards scientific progress.

A more complex and interesting monarch butterfly life history emerges from consideration of all "factors" that have influenced its evolution and stability. These selective factors may interact, and often encompass many interrelated forc-



Fig. 11. Male *D. plexippus* in flight with female (hanging) soon after mating has been initiated. Copulation will continue for 6 to 18 hours once a suitable resting site has been located by the male.

es. For example, summer food plant distributions, restricted wintering areas, and endocrine physiology combine to define range, limit oviposition, and cyclically shift geographic population centers. Ecological chemistry, predation deterrence, and mimicry relate not only to the aspects of the life history just mentioned but also influence predator types and potential mimics (Batesian, Mullarian, or Auto-; Ritland and Brower 1991). Aggregate overwintering reflects energetics, multiple mating, and second order breeding dynamics, as well as climatic and physiographic considerations.

The picture of monarch butterfly biology presented here is neither definitive nor complete. It can be improved by continued research effort, most rapidly if that picture is never so certain that falsification and strong inference approaches are considered out of order (Wenner and Wells 1990).

California provides a natural laboratory for the study and management of the monarch butterfly; winter aggregation, spring multiple mating, and summer oviposition all occur locally. Most of California's winter monarch aggregations occur in man-made groves of trees. Thus, a well-informed management could include successful planting of new forests, and deterioration of existing sites could be controlled. Supply side management should involve deliberate nurturing of milkweed patches in parklands and rural areas, with wider use of ornamental *Asclepias* in urban-suburban landscaping.

Californians can live in harmony with the magnificent monarch through continued research, management based on the knowledge gained through scientific study, and public awareness. Finally, the lessons learned in California will be

applicable, perhaps critical, in the battle to preserve the world's other monarch butterfly populations.

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Pleistocene Terrestrial Vertebrates from near Point San Luis, and Other Localities in San Luis Obispo County, California

George T. Jefferson,¹ Harry L. Fierstine,² John R. Wesling,³ and Teh-Lung Ku⁴

¹*George C. Page Museum, Los Angeles, California 90036*

²*School of Science and Mathematics, California Polytechnic State University,
San Luis Obispo, California 93407*

³*Geomatrix Consultants, San Francisco, California 94111*

⁴*Department of Geological Sciences, University of Southern California,
Los Angeles, California 90089*

Abstract.—Terrestrial vertebrate remains were recovered from sediments that lie on remnants of the lowest marine wave-cut platform between Point Buchon and Point San Luis. Uranium series ages of these samples, which range from 83 to about 49 ka suggest a correlation to late Pleistocene climatic and eustatic events associated with marine oxygen isotope substage 5a, and establish a maximum age of ≈ 80 ka for the occurrence of terrestrial mammal fossils. The Point San Luis area assemblage appears typical of the late Pleistocene regional vertebrate paleofauna from west-central California. Five mammalian taxa are added to the Pleistocene record from San Luis Obispo County. *Equus* sp. cf. *E. occidentalis*, *Camelops* sp. cf. *C. hesternus*, and *Bison antiquus* were recovered from the Point San Luis area, and *Mammuth americanum* and *B. latifrons* from near Morro Bay and the Carrizo Plains in eastern San Luis Obispo County.

Emergent marine terraces occur along most of the central California coastline (Veeh and Valentine 1967; Cleveland 1978; Weber 1983; Kennedy et al. 1988; Pacific Gas and Electric Company 1988; Hanson et al. 1990). A flight of at least twelve terraces is present between Morro Bay and Pismo Beach, north of Santa Maria Valley (Fig. 1). Hanson et al. (1990) mapped these terraces in detail and estimated the ages of marine terraces in this area using a variety of dating techniques, including: uranium-series disequilibrium of coral and bone, amino acid racemization, marine terrace altitudinal spacing, and paleoclimatic interpretation of marine invertebrate assemblages. The results of these studies suggest that the terraces from Morro Bay to the Santa Maria Valley range in age from greater than 1.0 Ma to approximately 80 ka.

Terrestrial and marine vertebrate fossils at three sites near Point San Luis (Fig. 2) were recovered from surficial deposits that lie above the abrasion platform of the lowest terrace. This wave-cut platform was formed during a high sea-level stand that has been correlated with marine oxygen isotope substage 5a of Shackleton and Opdyke (1973), and is estimated to be 80–85 ka old (Pacific Gas and Electric Company 1988; Hanson et al. 1990). Uranium series (U/Th) dates on these fossils range from 83 to about 49 ka.

In this paper we describe the taxa from the Point San Luis area. This assemblage

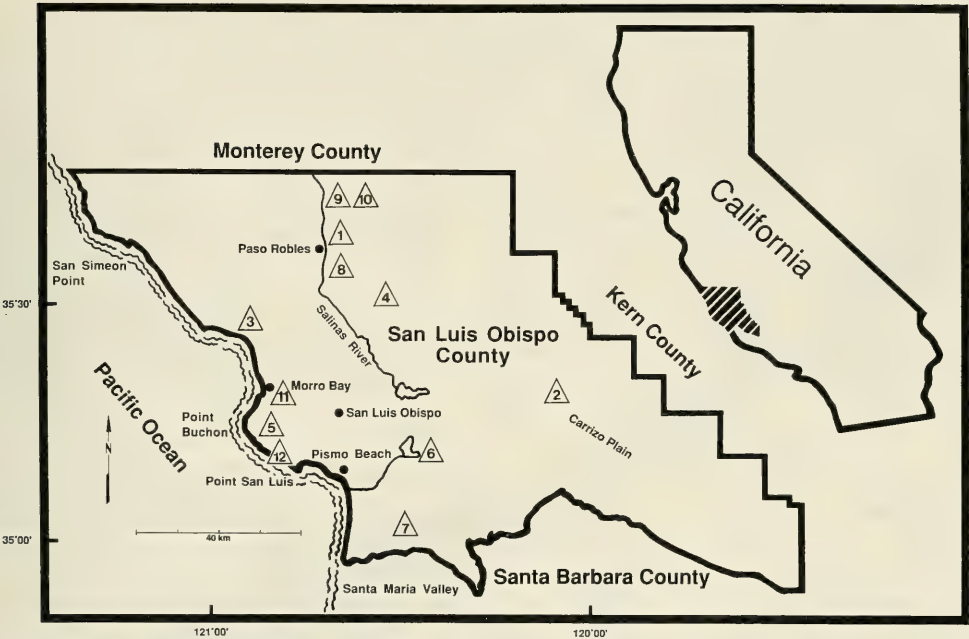


Fig. 1. Map of Rancholabrean Age (late Pleistocene) terrestrial vertebrate localities in San Luis Obispo County, California. Numbered triangles refer to California Polytechnic State University, San Luis Obispo (CPVP), Natural History Museum of Los Angeles County Vertebrate Paleontology Section (LACM), Museum of Paleontology (UCMP), or United States Geological Survey (USGSM) localities. Assemblages are listed in Table 1. Explanation: 1 = CPVP 6901, LACM 5791; 2 = CPVP 7803, LACM 5659; 3 = LACM 1720; 4 = CPVP 7802; 5 = LACM 4523, 4984, USGSM 7280; 6 = CPVP 6903, LACM 5790; 7 = LACM 4089; 8 = CPVP 7801; 9 = CPVP 6902; 10 = UCMP V65046; 11 = CPVP 7001, LACM 5903; 12 = Point San Luis localities. See Fig. 2 for the location of LACM 5800, 5801, and 5802.

provides a basis for the first description of Rancholabrean Age (late Pleistocene) mammals from San Luis Obispo County, California. In addition, we also report on late Pleistocene taxa from other, previously unreported sites in San Luis Obispo County, including the Chorro Creek locality near Morro Bay and the Carrizo Plains School locality in the eastern part of the county (Fig. 1). Table 1 presents a summary of vertebrate taxa from these localities and other localities in San Luis Obispo County.

Geologic Setting and Stratigraphy: Point San Luis Locality

Exposures of the lowest marine terrace typically exhibit three geologic features: 1) a wave-cut platform developed across Jurassic/Cretaceous Franciscan Formation and/or Cretaceous sandstone bedrock, 2) near-shore marine lag deposits, and 3) alluvium and/or colluvium (Fig. 3). The marine lag deposits average about 1 m in thickness and rest on the wave-cut platform. These marine sediments consist of cobbles and poorly-sorted gravels in a sandy matrix. Boulders up to 1 m in diameter may be present locally. In general, 10 to 20 m of alluvium and/or colluvium overlie the near-shore marine sediments. Where marine deposits are absent, terrestrial sediments lie directly on the wave-cut platform.

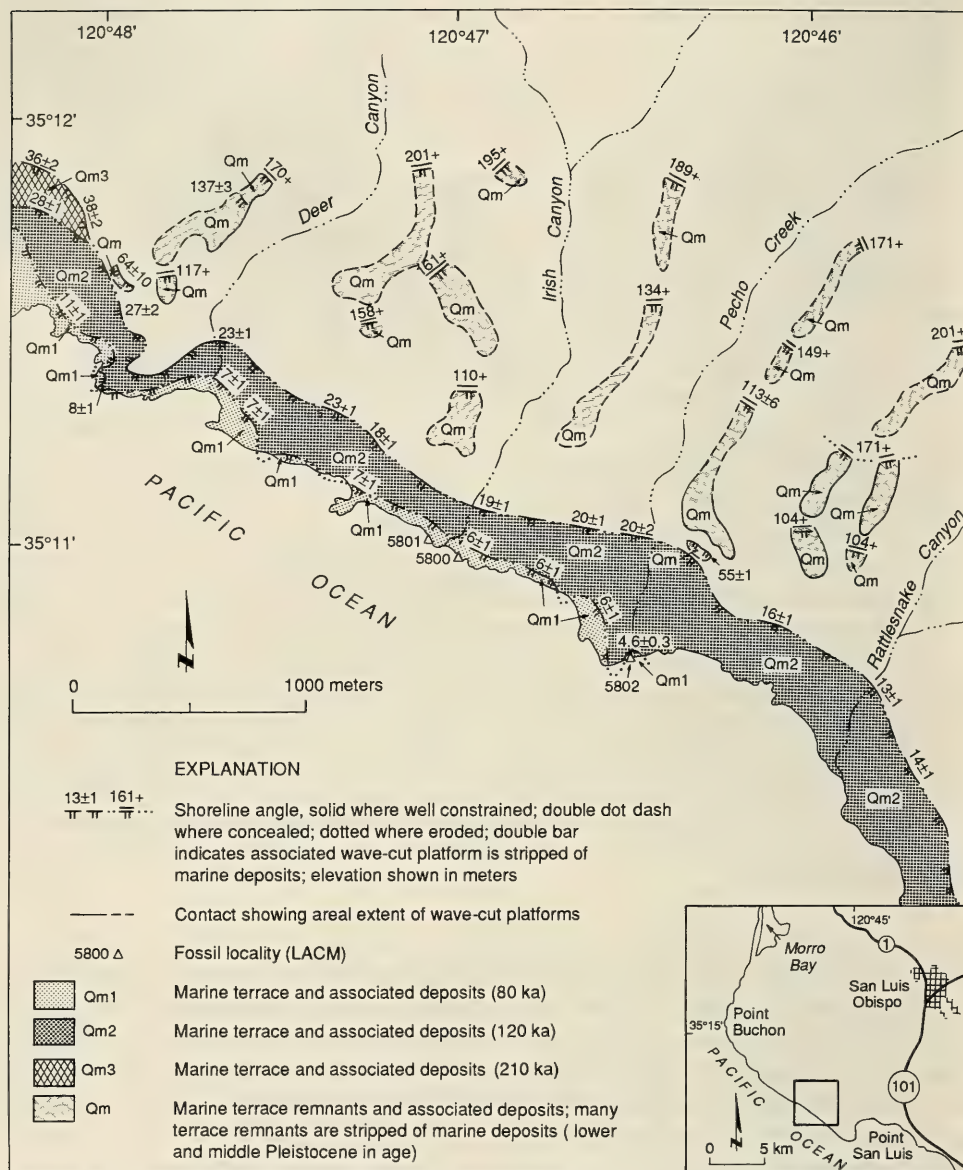


Fig. 2. Map of Quaternary marine terraces and late Pleistocene terrestrial vertebrate fossil localities northwest of Point San Luis, California (modified from Hanson et al. 1990). Locality numbers are from the Natural History Museum of Los Angeles County, Vertebrate Paleontology Section (LACM).

Vertebrate remains have been recovered from both marine lag deposits and alluvial sediments that lie on the lowest wave-cut platform. Natural History Museum of Los Angeles County (LACM) Vertebrate Paleontology Section locality 5802 is in a sea-cliff exposure adjacent to the east side of the mouth of Pecho Creek, 3.8 km northwest of Point San Luis (Fig. 2). Here, the exposed wave-cut platform is eroded into Cretaceous sandstone at an elevation of 4.6 ± 1.0 m above mean sea-level (MSL). The platform is covered with 80 cm of near-shore

Table 1. Late Pleistocene localities and vertebrate taxa from San Luis Obispo County. Abbreviations: CPVP = California Polytechnic State University San Luis Obispo vertebrate paleontology locality number; LACM = Natural History Museum of Los Angeles County, Vertebrate Paleontology Section locality number; LACMIP = Natural History Museum Los Angeles County, Invertebrate Paleontology Section locality number; UCMP = University of California Museum of Paleontology, Berkeley, locality number; USGSM = United States Geological Survey, Denver locality number (for map locations see Figs. 1 and 2).

Arbogast Ranch, Salinas River Valley: CPVP 6901; LACM 5791
<i>Mammuthus</i> sp.
<i>Equus</i> sp. cf. <i>E. occidentalis</i>
<i>Bison</i> sp. cf. <i>B. antiquus</i>
Carizzo Plains School, Carrizo Plains: CPVP 7803; LACM 5659
<i>Mammut americanum</i>
<i>Mammuthus</i> sp.
<i>Camelops</i> sp.
<i>Bison latifrons</i>
Chorro Creek, Morro Bay, coastal San Luis Obispo County: CPVP 7001; LACM 5903
<i>Mammut americanum</i>
Cayucos, South 5th Street, coastal San Luis Obispo County: LACM 1720
Sciuridae
Creston Mammoth Site, north-central San Luis Obispo County: CPVP 7802
<i>Mammuthus</i> sp.
Crowbar Canyon (Montana de Oro State Park) (C�nada Los Osos), Point Buchon area: LACM 4523, 4984; LACMIP 5640; USGSM 7280
? <i>Microgadus</i> sp.
Mammalia
Irish Canyon, northwest of canyon mouth, Point San Luis area: CPVP 8702; LACM 5801
<i>Bison antiquus</i>
Irish Canyon, southeast of canyon mouth, Point San Luis area: LACM 5800
<i>Equus</i> sp. cf. <i>E. occidentalis</i>
Mankin, Ranchita Cattle Company, southwestern San Luis Obispo County: CPVP 6903; LACM 5790
<i>Mammuthus</i> sp.
Nipomo, southwestern San Luis Obispo County: LACM 4089
<i>Mammuthus</i> sp.
Pecho Creek, southeast of canyon mouth, Point San Luis area: CPVP 8701; LACM 5802
<i>Glossotherium harlani</i>
Delphinidae
? <i>Equus</i> sp.
<i>Camelops</i> sp. cf. <i>C. hesternus</i>
Pecho Creek, point west of canyon mouth, Diablo Canyon area: LACM 5831
<i>Hydrodamalis</i> sp.
Point San Luis, coastal San Luis Obispo County: LACM 5803
Cetacea
Salinas River Sand Site, Salinas River Valley: CPVP 7801
<i>Mammuthus</i> sp.
San Miguel, Salinas River Valley: CPVP 6902
<i>Mammuthus</i> sp.
San Miguel, Salinas River Valley: = ? CPVP 6902 (Durham 1974)
<i>Mammuthus</i> sp.
San Miguel 2, Salinas River Valley: UCMP V65046
Camelidae

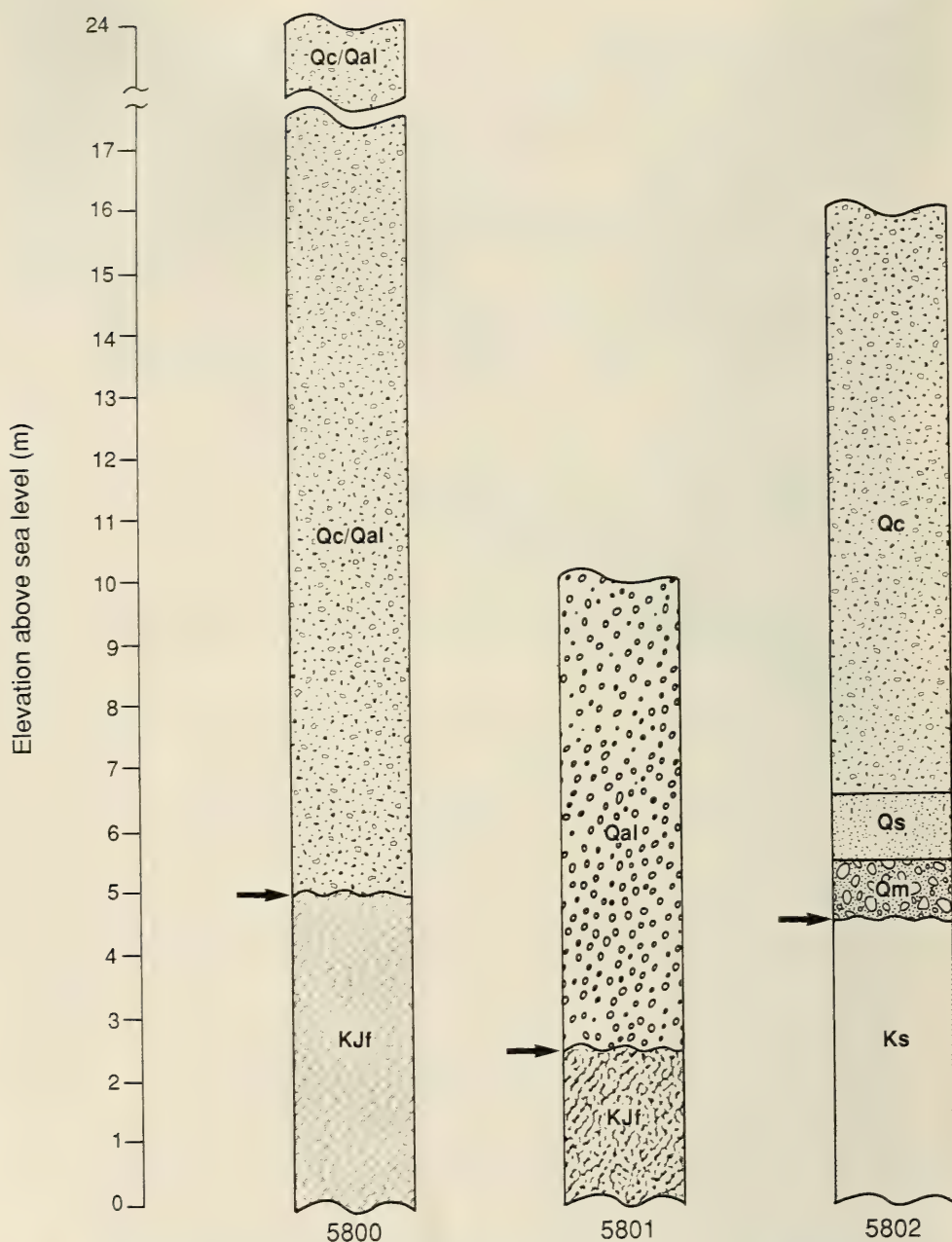


Fig. 3. Stratigraphic columns for late Pleistocene terrestrial vertebrate localities northwest of Point San Luis, California. Vertical scale in meters above mean sea-level. Locality numbers are from the Natural History Museum of Los Angeles County, Vertebrate Paleontology Section (LACM). Arrows indicate position of wave-cut platform. See text for more complete description of lithologies. Columnar section at: LACM 5800, east Irish Canyon; LACM 5801, west Irish Canyon; LACM 5802, Pecho Creek. Abbreviations: KJf = Cretaceous/Jurassic Franciscan Formation, Ks = Cretaceous sandstone, Qal = Quaternary alluvium, Qc = Quaternary colluvium, Qm = Quaternary marine lag deposit, Qs = Quaternary near-shore deposit.

marine, poorly-sorted sandy gravels that contain locally derived clasts of Cretaceous sandstone (90 percent), Jurassic/Cretaceous Franciscan Formation (7 percent) and various middle Tertiary rocks (3 percent). A 1 m-thick layer of sand overlies the marine lag deposit. This near-shore sediment is fine to medium-grained, well-sorted and contains some pebbly lenses up to 10 cm thick. About 10 m of colluvium is present above the marine deposits. This material consists of poorly-bedded, poorly-sorted, clayey, silty and gravelly sands with abundant lenses of both angular and rounded gravels (Fig. 3). A delphinid (dolphin) tooth (LACM 129919) from the near-shore, sandy deposits yielded a U/Th age of 82.8 ± 3.4 ka BP (USC W87-101) (Table 2).

Locality LACM 5800 is 4.7 km northwest of Point San Luis in a sea-cliff exposure adjacent to the east side of the mouth of Irish Canyon (Fig. 2). Near-shore marine deposits are absent here. The wave-cut platform is eroded into Jurassic/Cretaceous Franciscan Formation bedrock at an elevation of 4.9 ± 1.0 m above MSL, and is overlain by approximately 19 m of alluvium and colluvium (Fig. 3). The alluvial/colluvial deposits consist of poorly-bedded, moderately- to poorly-sorted, subangular to subrounded sandy gravels and gravelly cobble conglomerates. A partial right dentary of a juvenile *Equus* cf. *E. occidentalis* (LACM 129904) was collected from the gravels 30 cm above the wave-cut platform. The specimen does not exhibit abrasion typical of stream transport. A U/Th age of 61.5 ± 2.0 ka BP (USC W87-61) (Table 2) was obtained from the DP₂ of this specimen.

Locality of LACM 5801 is 4.8 km northwest of Point San Luis in a sea-cliff exposure adjacent to the west side of the mouth of Irish Canyon (Fig. 2). The platform is cut into Jurassic/Cretaceous Franciscan Formation bedrock at an elevation of 4.9 ± 1.0 m above MSL, and is overlain by approximately 7–8 m of alluvium (Fig. 3). The basal 5 m of the alluvium consists of moderately to well-sorted sand and gravel deposits. The sands are locally cross-bedded and clasts in the gravels are imbricated suggesting transport down Irish Canyon. Individual gravel deposits appear as irregular wedges that represent fluvial channel fills. A left dentary of *Bison antiquus* (LACM 129905) was recovered from the base of one of these gravel units 10 cm above the wave-cut platform. Lack of abrasion suggests little stream transport. An age of 50.6 ± 1.7 ka (USC W87-62) (Table 2) was obtained from a fragment of the P₃ from this specimen.

Systematic Descriptions

Family MYLODONTIDAE

Genus *Glossotherium* Owen, 1840

Glossotherium harlani (Owen), 1840

Referred material.—Locality LACM 5802; LACM 129907 fragment of right palatine, LACM 129908 5th cervical vertebra, LACM 129909 thoracic vertebra, LACM 129910 thoracic vertebra, LACM 129911 fragment of thoracic vertebra, LACM 129913 proximal portion of right scapula, LACM 129912 fragment of articular surface right scapula, LACM 129914 right ulna, LACM 129916 left femur, LACM 129915 terminal phalanx of right digit III manus, and LACM 129917 rib fragments.

Discussion.—The specimens are morphologically indistinguishable from *Glos-*

Table 2. Radiochemical and age results on vertebrate specimens from the Diablo Canyon area. Sample numbers are from the University of Southern California (USC) Department of Geology. Explanation: USC 524P-A = LACM 5831/129941; USC W87-61 = LACM 5800/129904; USC W87-62 = LACM 5801/129905; USC W87-101 = LACM 5802; USC W87-103 = LACM 5803/129920.

Sample no.	Material	Organics* (%)	U (ppm)	$^{234}\text{U}/^{238}\text{U}$	$^{230}\text{Th}/^{232}\text{Th}$	$^{230}\text{Th}/^{234}\text{U}$	$^{231}\text{Pa}^\dagger/^{235}\text{U}$	Ages (ka)	
								Th/U	Pa/U
524P-A	Cetacea Rib	5.8	140 ± 1	1.01 ± 0.01	780 ± 102	0.364 ± 0.012	0.659 ± 0.024	49.0 ± 0.8	50.9 ± 3.5
W87-61	Horse dentary	8.2	121 ± 1	1.02 ± 0.02	155 ± 16	0.434 ± 0.010	0.751 ± 0.023	61.5 ± 2.0	65.8 ± 4.4
W87-62	Bison dentary	5.0	70.4 ± 0.7	1.02 ± 0.01	258 ± 63	0.373 ± 0.010	0.599 ± 0.024	50.6 ± 1.7	43.3 ± 2.9
W87-101	Delphinid teeth	5.7	60.8 ± 1.3	1.04 ± 0.02	201 ± 37	0.535 ± 0.015	0.901 ± 0.069	82.8 ± 3.4	109 ± $^{+33}_{-23}$
W87-103	Cetacea Rib	12.1	146 ± 1	1.22 ± 0.01	170 ± 20	0.449 ± 0.008	0.709 ± 0.020	63.3 ± 1.5	58.5 ± 3.3

* Weight loss after ashing at 450°C.

† Measured via ^{227}Th analysis.

sotherium harlani, and fall within the size range of individuals in the Rancho La Brea population. At least three individuals are represented: one juvenile and two adults. The juvenile specimens include an ulna (LACM 129914) which is missing the distal articular epiphysis, and cervical vertebra (LACM 129908) that lacks a posterior centrum epiphysis. Parts of two adult right scapulae were recovered (LACM 129912 and LACM 129913).

The remains of *Glossotherium harlani* are not uncommon in upper Pleistocene, near-shore marine deposits of coastal southern California (Miller 1971; Langenwalter 1975). Even though this constitutes the first record of *G. harlani* in San Luis Obispo County (Table 1), this species is known from other sites in west-central California including Carpinteria, Los Alamos, and Point Sal in Santa Barbara County, and Bolsa Chica State Park in Ventura County (Table 4).

Family EQUIDAE

Genus *Equus* Linnaeus, 1758

Equus sp. cf. *E. occidentalis* Leidy, 1865

Referred material.—LACM 5800/129904 right dentary fragment with DP₂₋₄ and partially formed P₃₋₄, LACM 5802/129918 rib fragment.

Discussion.—Although the taxonomic status of *Equus occidentalis* is uncertain (Miller 1971), this specific name has been used to describe the extinct horse from Rancho La Brea. The name is applied here to specimens comparable to those from Rancho La Brea.

DP₃ and DP₄ in LACM 129904 are very well worn, with crown heights of 13 and 17 mm, respectively. The anterior-posterior diameter of DP₃ is 33.1 mm and the lingual-labial diameter is 17.6 mm. The anterior-posterior diameter of DP₄ is 35.3 mm, and the lingual-labial diameter is 17.5 mm. The unerupted crowns of P₃₋₄ were recovered, but the other, more posterior teeth were not preserved. The DP₂ was destroyed during U/Th analysis (Table 2) and was not available for study. The rib fragment, LACM 129918 is not diagnostic at the specific level.

Materials referred to *Equus occidentalis* are common in upper Pleistocene deposits of coastal central and southern California. However, this taxon has not been reported previously from San Luis Obispo County. It is now represented by LACM 5800/129904 and a right M₂ (LACM 129922) and thoracic vertebra (LACM 129923) from the Arbogast Ranch locality (LACM 5790) in the Salinas River Valley (Fig. 1, Table 1). *Equus* is known from many localities in Ventura County, and occurs at Carpinteria, Los Alamos, and Point Sal in Santa Barbara County (Table 3).

Family CAMELIDAE

Genus *Camelops* Leidy, 1854

Camelops sp. cf. *C. hesternus* (Leidy), 1873

Referred material.—LACM 5802/129906 left innominate.

Discussion.—Fusion of the ilium and ischium is nearly complete suggesting a subadult individual. The specimen is comparable in size to that of the smallest adult specimens from Rancho La Brea. Anterior-posterior diameter of the acetabulum is 74 mm.

The remains of *Camelops hesternus* are not as well represented in upper Pleistocene deposits from coastal southern California as are other large herbivores

Table 3. Late Pleistocene terrestrial mammalian fauna of west-central California. F = family present; G = genus present; M = Monterey County; S = genus and species present; SBN = San Benito County; SBR = Santa Barbara County; SLO = San Luis Obispo County; V = Ventura County.

SLO taxa	M	SBR	SBN	V
<i>Glossotherium harlani</i>	S	S	—	G
Sciuridae	F	—	—	—
<i>Mammuth americanum</i>	—	S	S	G
<i>Mammuthus</i> sp.	—	G	G	G
<i>Equus occidentalis</i>	G	S	G	S
<i>Camelops hesternus</i>	G	G	—	G
<i>Bison antiquus</i>	G	G	—	G
<i>B. latifrons</i>	S	G	—	G

such as *Glossotherium*, *Equus* or *Bison* (Marcus 1960; Jefferson 1988). *C. hesternus* (left innominate fragment, LACM 129896) has also been recovered from the Carrizo Plains School locality (LACM 5659) (Fig. 1, Table 1) in eastern San Luis Obispo County. The taxon is also known from Carpinteria, and Conception Station in Santa Barbara County, and from the city of Ventura in Ventura County (Table 3). This is the first report of this species from San Luis Obispo County.

Family BOVIDAE

Genus *Bison* Smith, 1827

Bison antiquus Leidy, 1857

Referred material.—LACM 5801/129905 left dentary with P_2 , P_4 and M_{2-3} .

Discussion.—LACM 5801/129905 represents a large, mature individual. The hypoconulid of the M_3 exhibits slight wear and is connected to the entoconid and hypoconid by a continuous wear facet. Depth of the dentary measured below the metaconid of M_3 is 83.5 mm. The M_1 was not preserved, and a fragment of the P_3 was used to obtain a U/Th determination (Table 2) before measurements could be taken. Dimensions of the recovered teeth are given in Table 4.

This dentary and the proximal end of a left metatarsal (LACM 129921) from the Arbogast Ranch locality (LACM 5791) (Fig. 1, Table 1) are the first records of *Bison antiquus* from San Luis Obispo County. The taxon is commonly found in upper Pleistocene deposits along the southern California coast. It is known from Carpinteria and Point Sal in Santa Barbara County, and from Chandler's Sand Pit, Bolsa Chica State Park, and Pier Point Bay in Ventura County (Table 3).

Table 4. Dimensions (in mm) of *Bison antiquus* lower dentition LACM 5801/129905. Measurements taken at the level of the alveolar border, AP = maximum anterior-posterior diameter, LL = maximum lingual-labial diameter.

	AP	LL
P_2	15.3	10.2
P_4	26.3	15.5
M_2	38.0	19.5
M_3	47.7	17.5
M_{2-3}	85.3	

Radiometric Dating Methods and Results

Each vertebrate specimen was radiometrically dated by both $^{230}\text{Th}/^{234}\text{U}$ and $^{231}\text{Pa}/^{235}\text{U}$ methods (Ku 1976) in order to check concordancy between the two independent age estimates. The analyses were done as follows. The cleaned, powdered bone samples were first ashed at 450 degrees Celsius to remove organic matter. The remaining fraction (ashed inorganic bone) was then dissolved in nitric acid. For each sample, the solution was split into two aliquots: one was spiked with a $^{232}\text{U}/^{228}\text{Th}$ tracer for $^{230}\text{Th}/^{234}\text{U}$ determination and the other was spiked with ^{236}U and ^{229}Th tracers for $^{227}\text{Th}/^{235}\text{U}$ determination. It was assumed that ^{231}Pa was in secular equilibrium with ^{227}Th in the samples, so that the measured ^{227}Th activities represent those of ^{231}Pa (Gascoyne 1985). Both determinations were done using alpha-spectrometry, after thin sources of purified U and Th were made.

Radiometric age data are listed in Table 2. The uranium data (ppm U and $^{234}\text{U}/^{238}\text{U}$ activity ratios) are mean values of measurements made on the two aliquots. The uncertainties assigned are one standard deviation from the mean. Uncertainties in the two aliquots are the same magnitude, implying excellent reproducibility in the measurements and that counting statistics based on single runs are valid precision estimates.

The results listed in the last two columns of Table 2 indicate that, except for sample USC W87-62, all samples show concordant $^{230}\text{Th}/^{234}\text{U}$ and the $^{231}\text{Pa}/^{235}\text{U}$ ages that agree to within one-sigma analytical error limits. However, the two ages for USC W87-62 still agree within two-sigma errors. The age concordancy and the large $^{230}\text{Th}/^{232}\text{Th}$ activity ratios (Table 2) serve to validate the method's two assumptions: the samples remained as a closed system with respect to U, Th and Pa isotopes during their burial, and the measured ^{230}Th and ^{231}Pa are mostly produced *in situ* by decay of uranium in the samples.

The $^{230}\text{Th}/^{234}\text{U}$ ages are preferred to their $^{231}\text{Pa}/^{235}\text{U}$ age counterparts, because they are more precise and because the assumed equilibrium between ^{227}Th and ^{231}Pa adopted in the $^{231}\text{Pa}/^{235}\text{U}$ age determination, though highly probable, is still an assumption. The majority of uranium in bones is taken up *post mortem* (Ku 1976). The time lapse between death/burial and uranium uptake is assumed to be short relative to the ages of the samples. Therefore, the ages reported here are minimum estimates that approximate the time of death. Given rapid uranium uptake, dates for samples older than about 20 ka should be reliable (Schwarcz 1982).

Discussion: Regional Paleofauna

The terrestrial vertebrates recovered from the Point San Luis area add to the paleontologic record from coastal central California. Four taxa from these sites, *Glossotherium harlani*, *Equus occidentalis*, *Camelops hesternus*, and *Bison antiquus* previously have not been reported from San Luis Obispo County.

Within San Luis Obispo County and west-central California, all remains of *Glossotherium harlani* have been recovered from coastal sites. Apparently, this is the only extinct large mammal within the region that exhibits a restricted geographic range.

Mammuthus sp. commonly occurs in Pleistocene sites throughout San Luis

Table 5. Dimensions (in mm) of *Bison latifrons* axis and fourth cervical vertebrae LACM 5659/129895. For comparative measurements of *Bison* axis vertebrae see Miller (1968).

Axis vertebra	
Greatest length of centrum from base of odontoid process to posterior articular surface	162+
Maximum transverse width of odontoid process	60
Height of neural spine from superior border of neural arch to dorsal tip of spine	84+
Transverse width of anterior articular surface	142
Dorso-ventral diameter of posterior articular surface	70
Transverse diameter of posterior articular surface	66
Fourth cervical vertebra	
Greatest length of centrum	123
Dorso-ventral diameter of anterior articular surface	65
Transverse diameter of anterior articular surface	42
Dorso-ventral diameter of posterior articular surface	71
Transverse diameter of posterior articular surface	64
Transverse width across prezygapophyses at dorsal margin	141
Transverse width across postzygapophyses at ventral margin	150

Obispo County (Table 1), but was not recovered from the Point San Luis area. This taxon is known from numerous other late Pleistocene terrestrial and near-shore deposits in southern and central California (Miller 1971; Langenwalter 1975) (Table 3).

Mammuth americanum has been recovered from two sites, Chorro Creek near Morro Bay (LACM 5903), and the Carrizo Plains School locality (LACM 5659) in eastern San Luis Obispo County (Fig. 1, Table 1). This taxon occurs at other localities throughout coastal southern California (Table 3), but is not represented in eastern, inland California assemblages (Jefferson 1989).

Bison latifrons was recovered from the Carrizo Plains School locality. The taxon is known from localities throughout northern California. However, it was not found in the Point San Luis area, and is poorly represented in other coastal southern California assemblages (Miller 1968, 1971). *B. latifrons* is reported from only one other locality in east-central and southeastern California (Jefferson 1971).

Because *Bison latifrons* is rare in southern California, the axis and fourth cervical vertebrae of a single individual (LACM 129895) from the Carrizo Plains School locality (LACM 5659) (Fig. 1, Table 1) warrant a brief description. These vertebrae are much larger than those of *B. antiquus*, and compare favorably with *B. latifrons* from Rancho La Brea. Some osteologic parameters of these vertebrae (Table 5) exceed the dimensions of *B. latifrons* reported by Miller (1968).

The late Pleistocene mammalian paleofauna from San Luis Obispo County is not significantly different from that recorded for the west-central region of California. All large species are also known from Santa Barbara and Ventura Counties (Table 3).

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Aquatic Invertebrates Inhabiting Saline Evaporation Ponds in the Southern San Joaquin Valley, California

Michael S. Parker and Allen W. Knight

*Department of Land, Air, and Water Resources,
University of California at Davis, Davis, California 95616*

Abstract. — A large number of shallow evaporation basins are currently being used to dispose of subsurface agricultural drain water in the southern San Joaquin Valley of California. The proliferation of ponds has led to an increase in shallow, saline aquatic habitats in this arid region of the state. During spring and summer 1987 we conducted a survey of three pond systems to describe invertebrate assemblages inhabiting them. Because of relatively high salinities, evaporation ponds are harsh environments for most aquatic organisms. We found all ponds to have macroinvertebrate and zooplankton assemblages of very low diversity and there was a negative correlation between taxonomic diversity and salinity. Characteristic invertebrates among ponds included the water boatman *Trichocorixa reticulata*, Chironomidae (predominantly *Tanypus* sp.), brineflies (genus *Ephydra*), and the halophillic rotifer *Brachionus plicatilis*.

A long-standing problem for farmers in the southern San Joaquin Valley of California has been the disposal of subsurface irrigation drain water. Many farmers currently dispose of these effluents in shallow evaporation ponds. At present there are 27 evaporation pond systems in operation in Kings, Tulare, Fresno, and Kern Counties. Evaporation ponds range from small single cell systems less than 10 hectares in size to large, multi-cell systems greater than 500 hectares in size. Currently, the total area occupied by evaporation ponds is approximately 2900 hectares. However, the California Department of Water Resources and U.S. Fish and Wildlife Service predict that within 10 years evaporation ponds could increase to a total area of 12,000 hectares.

The proliferation of evaporation ponds in the southern San Joaquin Valley has led to a dramatic increase in shallow, saline aquatic habitats in this arid region of the state. Physical characteristics of evaporation ponds have been described (Tanji et al. 1985), yet there have been no published studies describing evaporation pond biota. Here we present a brief description of invertebrate assemblages inhabiting three evaporation pond systems varying widely in concentrations of dissolved solutes, and representing a range of conditions among ponds currently in operation.

Methods

The three pond systems we surveyed were: (1) Barbizon Pond, a 41.3 hectare single cell system located in north-central Kings County, (2) Sumner-Peck Ponds, a 42.5 hectare, 5 cell system located in SW Fresno County, and (3) Pryse Ponds, a 33.6 hectare, 2 cell system located in SW Tulare County. As is characteristic of

all evaporation ponds, these three systems were shallow (0.25 to 1.5 m deep) with extensive surface area relative to storage volume. Concentrations of dissolved solutes varied considerably among the three systems and among cells of the multi-cell systems (Table 1). In the multi-cell systems drain water enters the first cell and is routed sequentially into the other cells establishing a gradient of increasing solute concentrations across them. The pH was between 8.5 and 9.5 in cells of all three systems, and mid-day temperatures ranged from 20°C to 28°C during our survey. Faunal assemblages inhabiting the hypersaline Pryse system are likely to be similar to assemblages that will develop in most evaporation ponds as solutes within them become concentrated over time.

Our primary objective was to make a qualitative description of evaporation pond invertebrate assemblages and compare their distributions among ponds with widely varying dissolved solute concentrations. We collected samples of pond invertebrates on 16–17 May (spring) and 05–06 August 1987 (summer). We restrict our discussion here to the spring and summer because productivity within the ponds is highest during these seasons and invertebrate densities and diversity are greatest (Parker and Knight 1989). By collecting a large number of samples from many locations within each pond we were able to establish a complete list of taxa inhabiting them (Elliott 1977). Although this type of biological survey precludes making quantitative estimates of population densities, we were able to determine which taxa had the highest relative abundances and thus make qualitative descriptions of pond communities.

We sampled benthic and nectonic macroinvertebrates with a D-frame dip net (0.6 mm mesh) by sweeping it horizontally through the top 3 to 5 cm of sediment (approximately 1 m per sweep) and then lifting it vertically through the water column. This procedure was repeated twice at a minimum of three sites equally spaced along transects bisecting each pond and at six to ten sites around pond margins. In addition, at each sample location we made several sweeps through the water column above the sediments. Material collected in the net was washed onto a 0.6 mm sieve and rinsed to remove fine sediments. The remainder of the material was preserved with 80% ethyl alcohol and returned to the laboratory where all invertebrates were hand sorted from debris under 10× magnification and identified to the lowest possible taxonomic level.

We collected planktonic invertebrates with a Van Dorn water sampler and by making three vertical tows with a standard plankton net (52 µm mesh) at three locations equally spaced along transects bisecting each pond. These samples were also preserved with 80% ethyl alcohol and returned to the laboratory for identification.

Results

Table 2 summarizes the invertebrate taxa collected during this survey. In general, invertebrate assemblages in all ponds were of very low diversity, with one to at most three taxa comprising over 90% of the total density of planktonic, benthic and nectonic groups. Species richness was inversely related to salinity. The greatest number of taxa were collected from Barbizon Pond and Peck cells 1 and 2, which had relatively low salinities, and the hypersaline Pryse system had the fewest taxa.

The waterboatman, *Trichocorixa reticulata* (Hemiptera: Corixidae), was the

Table 1. Range in salinity (expressed as mg/l TDS) of three evaporation pond facilities as measured between May and August 1987.

Evaporation pond	Salinity (mg·l ⁻¹ TDS)
Barbizon Pond	18,367–18,709
Peck Ponds	
Cell 1	7,367–9,256
Cell 2	8,311–12,987
Cell 3	13,592–20,286
Cell 4	15,021–30,241
Cell 5	20,698–32,891
Pryse Ponds	
Cell 1	32,402–48,286
Cell 2	54,735–> 70,000§

§ Pryse pond cell 2 dried completely during August 1987.

most characteristic species of pond macroinvertebrate assemblages, occurring in all cells of all three pond systems. In addition, *T. reticulata* was often the dominant organism comprising as much as 70 to 90% of total macroinvertebrate density in most ponds. Other important taxa included the chironomid *Tanypus* sp. and the damselfly *Enallagma civile* in Barbizon Pond and Peck cells 1 and 2, and brine flies (genus *Ephydra*) in Peck cells 4 and 5 and both cells of Pryse. Adult brine flies were extremely abundant around the margins of all ponds. The remainder of the macroinvertebrate taxa listed in Table 2 made up less than 2% of total invertebrates collected.

Zooplankton assemblages varied both among cells within systems and among systems. Characteristic taxa included a small calanoid copepod, *Diaptomus* sp., which was the dominant plankter in Barbizon and cells 1 through 3 of the Peck system. The halophillic rotifer, *Brachionus plicatilis*, was present in all three systems and was the dominant plankter in Peck cells 3 through 5 and in both cells of the Pryse system. In May 1987 the brine shrimp, *Artemia salina*, was extremely abundant in cell 2 of the Pryse system.

Discussion

Biological features of evaporation ponds reflect the fact that they are harsh aquatic environments. As is typical of most harsh environments, species diversity within evaporation ponds is very low. Because most aquatic organisms have limited osmoregulatory abilities, high concentrations of dissolved minerals is likely the most important factor determining biological characteristics of these systems. The inverse relationship between species diversity and the concentration of dissolved minerals among evaporation ponds is typical of inland saline lakes in general (Hammer 1986; Rawson and Moore 1944; Williams 1981). Moreover, invertebrates inhabiting evaporation ponds belong to taxonomic groups that characterize invertebrate assemblages of saline lakes worldwide (Hammer 1986).

Although invertebrate species diversity was very low, population densities of dominant taxa appeared to be very high. Evaporation ponds have extensive surface areas relative to storage volumes, receive direct sunlight throughout the day, and receive irrigation drainage rich in nutrients (Johnson et al. 1965). These factors

Table 2. List of macroinvertebrate and zooplankton taxa collected from three evaporation pond facilities during spring (16–17 May) and summer (5–6 August) 1987. A = abundant taxa representing >25% of total organisms collected; C = common taxa representing between 1% and 24% of total organisms collected; P = organisms that were present but represented <1% of total organisms collected. Macroinvertebrate and zooplankton relative abundances estimated separately.

	Barbi- zon	Peck					Pryse	
		1	2	3	4	5	1	2
Macroinvertebrates								
Hemiptera								
<i>Trichocorixa reticulata</i>	A	A	A	A	A	A	A	A
<i>Buenoa scimitra</i>	P	P	P	P				
<i>Notonecta unifasciata</i>	P	P	P					
Diptera								
<i>Tanytus</i> sp.	A	A	A	C	P			
<i>Tanytarsus</i> sp.	P	C	C					
Other chironomidae	P	P	P					
Ceratopogonidae	P	P	P					
<i>Ephydra hians</i>	P	P	P	P	C	C		
<i>Ephydra cinerea</i>							A	A
Odonata								
<i>Enallagma civile</i>	C	C	C	P	P			
<i>Ischnura</i> sp.	P	P	P					
Coleoptera								
<i>Hydrophilus triangularis</i>	P	P						
<i>Hydrovatus brevipes</i>		P	P					
Ephemeroptera								
<i>Callibaetis</i> sp.		P	P					
Ostracoda								
	C	C	C	C	C	P		
Zooplankton								
Copepoda								
<i>Diaptomus</i> sp.	A	A	A	A	A	C		
<i>Cyclops</i> sp.	P							
Rotifera								
<i>Brachionus plicatilis</i>	C	P	P	C	C	A	A	A
Anostracoda								
<i>Artemia salina</i>								A
Cladocera								
<i>Chydorus</i> sp.			P					

combine to create conditions conducive to very high biological productivity, as is typical of shallow, saline aquatic systems in general (Hammer 1986; Williams 1981). Both planktonic and benthic algal densities were quite high in all ponds and were dominated by cyanobacteria (predominantly *Oscillatoria* spp. and *Spirulina* spp.) and numerous diatom taxa. *Ruppia maritima*, a submergent macrophyte common in saline aquatic habitats (Brock 1981; Hammer and Hazeltine 1988), was present in Peck cells 1 through 3 and was very dense in Barbizon Pond. This plant provides important substrate, cover, and oviposition sites for many macroinvertebrates inhabiting evaporation ponds. We estimated *T. reticulata* egg densities of 8 to 10 per cm² of *Ruppia* stem surface, and observed large numbers of *Ephydra hians* pupae attached to *Ruppia* stems in Barbizon Pond.

Ruppia does not occur in hypersaline systems (Brock 1981), and did not occur in cells 4 and 5 of the Peck system or in the Pryse ponds.

Because evaporation ponds are closed systems, concentrations of dissolved solutes will increase with time. Eventually all ponds will become hypersaline and invertebrate species diversity should decrease. This process may be somewhat slower, however, in initial cells of multi-cell systems that receive frequent inflows of relatively fresh drain water. Invertebrate assemblages similar to those in Bar-bizon Pond and cells 1 through 3 of the Peck system will likely be transient and will shift to resemble the Pryse ponds over time. Thus, dominant taxa likely to inhabit evaporation ponds in the future will include *B. plicatilis* and *A. salina* in the plankton and *T. reticulata* and *E. cinerea* in the benthos.

Although created as temporary disposal sites for agricultural effluents, evaporation ponds now represent a large proportion of aquatic habitats in the southern San Joaquin Valley, and will comprise an even greater proportion as more are built and put into operation. There is considerable concern that evaporation ponds pose an environmental hazard to migratory and resident waterfowl, shorebirds and other wildlife due to the uptake and accumulation, through aquatic food webs, of contaminants present at elevated levels in agricultural drainage. Descriptions of the biota inhabiting evaporation ponds is a first step in understanding the nature of these newly created aquatic systems. However, further research is necessary to determine potential negative impacts or benefits resulting from the use of evaporation ponds on a large scale.

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Research Note

The Feeding Preferences of the Sculpins, *Scorpaenichthys marmoratus* and *Leptocottus armatus*, between Sand Crangon and Small-eyed Shrimp, *Crangon nigricauda* and *Heptacarpus cf. carinatus*

Timothy R. McAdams,¹ Gigi Kroll,² and Keith Loehr³

Department of Biology, University of California at Los Angeles,
Los Angeles, California 90024-1606

¹20107 Mendelsohn Lane, Saratoga, California 95070

²24122 La Hermosa, Laguna Niguel, California 92677

³1015 Gayley Avenue #369, Los Angeles, California 90024

Scorpaenichthys marmoratus (cabezon) and *Leptocottus armatus* (Pacific staghorn sculpin) reside in shallow, inland bays along the California coast (Eschmeyer et al. 1983). These sculpins grow to 40 cm in length and are voracious feeders (Hart 1973). Most studies of the diet of sculpins have been conducted by examining the contents of their stomachs (Hart 1973). It is known that invertebrates (mainly crustaceans) comprise a major portion of the diet of these two species (Bane and Bane 1971). However, there are still many unanswered questions concerning the fishes' feeding behavior. The effects of camouflage, nutrition, toxicity, and prey density have remained largely unexplored.

Both *Heptacarpus cf. carinatus* (Small-eyed shrimp) and *Crangon nigricauda* (Sand crangon) are abundant in the eelgrass beds and sandy bottoms of Bodega Bay Harbor (personal observation), where staghorn sculpins and cabezons also reside. The Small-eyed shrimp have a bright green color, whereas the sand crangon shrimp are transparent. These are small crustaceans (less than 80 mm in length) that could serve as potential prey items. In this study, we observed in-vitro feeding habits of these fishes. We gave both cabezons and Pacific staghorn sculpins a choice between the two shrimp species and observed the proportion in which each shrimp species was taken.

Pacific staghorn sculpins were collected from Tomales Bay, Marin Co., California, using a 31 mm mesh beach seine. Additional Pacific staghorn sculpins and cabezons were collected at low tide from Campbell Cove, Sonoma County, California, using a 6 mm mesh seine. Voucher specimens of the Pacific staghorn sculpin and cabezon were deposited in the UCLA Ichthyology Research Collection, UCLA W90-17 and UCLA W90-16, respectively. Live fishes were kept in three Plexiglas tanks (45 cm × 45 cm, 20 cm deep) with four Pacific staghorn sculpins in Tank 1 and four cabezons of comparable size in each of Tanks 2 and 3. The tanks were cleaned at noon each day. The water level was maintained at just under 11 cm, an adequate distance below mesh-covered overflow holes as was necessary to prevent the shrimp from climbing out of reach of the fishes. Each tank was aerated for the duration of the experiment. Both shrimp species

were collected from Tomales Bay and Campbell Cove using seines and were kept in a large tank with circulating seawater. Voucher specimens of *Heptacarpus* cf. *carinatus* and *Crangon nigricauda* were deposited in the collection of the Natural History Museum of Los Angeles County, LACM 90-157.1 and LACM 90-157.2, respectively.

The sculpins were acclimated to the laboratory environment for two weeks prior to starting the experiment. They were fed unrestricted portions of both kinds of shrimp until two days prior to initiation of the experiment. Following an approximate 48 hour fasting period, ten shrimp (five of each species) were placed in each tank at 21:00. Subsequently, the total number of shrimp eaten was observed and recorded at twelve hour intervals (9:00 and 21:00).

At each observation time, new shrimp of similar sizes were added to replace the consumed individuals of each species. Data were collected for fifteen 12-hour periods for Tank 1, and twelve 12-hour periods for Tanks 2 and 3.

In all three tanks, the sculpins ate more *C. nigricauda* than *H. cf. carinatus* (Fig. 1). Chi-squared analyses yield values of $\chi^2 = 7.07, 7.86, 9.56$ for Tanks 1, 2, and 3, respectively. In all three cases $df = 1$ and $P < 0.05$. Cabezones and Pacific staghorn sculpins were observed eating a larger number of green shrimp on day one, as compared to any other day in the experiment (Fig. 2).

Pair-wise t-tests compared the numbers and species of consumed shrimp for Tanks 2 and 3, 1 and 3, and 1 and 2, which yield the following results, respectively: $t = 0.48, df = 82, P > 0.6$; $t = 0.469, df = 85, P > 0.6$; $t = 0.947, df = 83, P > 0.3$.

Both cabezones and Pacific staghorn sculpins ate significantly more *C. nigricauda* than *H. cf. carinatus*, and there were no significant differences in feeding preferences between tanks containing the same or different sculpin species. There are many possible hypotheses to explain why a preference existed. For one, there may be a mutualistic relationship between *H. cf. carinatus* and the sculpins. Often *H. cf. carinatus* were seen riding on the backs of the experimental fishes, where perhaps the shrimp were feeding upon external parasites. An example of such a mutualistic relationship is exhibited by the banded shrimp (*Stenopus hispidus*), which provide a cleaning service for fishes with wounds or parasites. In addition, the banded shrimp have distinctive coloration which helps the "patient" locate them (Bannister and Campbell 1985). Although *H. cf. carinatus* are brightly colored, this may also aid in camouflaging. In general, the *H. cf. carinatus* exhibited a "clinging" behavior not displayed by the *C. nigricauda*. *Heptacarpus* cf. *carinatus* were commonly seen clinging to the tubing or the airstone, to the backs of fishes, or to one another. This behavior may make them more difficult to capture than *C. nigricauda*. When *H. cf. carinatus* clung to one another, they appeared as a large mass that might have appeared intimidating to the fish. It was also observed that *H. cf. carinatus* preferred clinging on to green items, such as green airstones or handnets. The resulting camouflage could be an antipredation response, for these shrimp were taken from eelgrass beds, where the abundant green blades supply excellent cover. Indeed, eelgrass blades in the shrimp holding tank were always covered with clinging *H. cf. carinatus*, whereas the *C. nigricauda* were distributed more evenly throughout the tank. It is interesting to note one observation regarding camouflage. The experimental tanks were made of a thick, transparent plastic. While taking observations it was noted that *C. nigricauda* were

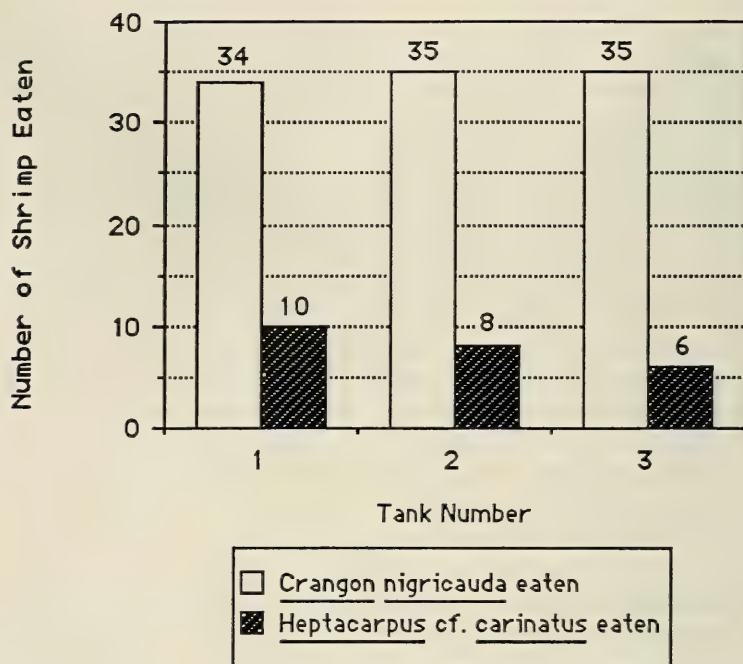


Fig. 1. Comparison of total green and sand shrimp consumed in Tanks #1, #2, and #3. Tank #1 contained *Leptocottus armatus* and Tanks #2 and #3 each contained *Scorpaenichthys marmoratus*.

much more difficult to see than the brightly colored green *H. cf. carinatus*. They were better “camouflaged” in the artificial environment, however they were nonetheless eaten in significantly larger numbers.

There may also be internal operational factors affecting the preference choices. For one there may be either nutritional, caloric, or taste differences between the two species that make one more favorable than the other. Because both prey items are present in the sculpin’s habitat, they may be able to distinguish which shrimp is more beneficial. Conversely, one shrimp may have a slightly negative nutritional factor, such as a toxin, that the fish chooses to avoid when other alternatives are present. Finally, it may simply be that *C. nigricauda* were easier to capture or to digest than *H. cf. carinatus*. In any case the sculpins may be choosing prey items that are more energetically favorable. Therefore the fish would be exhibiting an adaptive behavior that increases its overall fitness.

In any in vitro experiment it is important to question the external validity of the results. Although a significant difference did occur in the choice of prey items, this may not be ecologically significant. For example, prey availability in the natural environment may be so low that the fish feeds indiscriminately, consuming any prey item it encounters. However, if prey items are abundant then it may be energetically advantageous for the fish to be selective. This possible trend was noticed at the beginning of the experiment. Although the sculpins were acclimated to laboratory conditions for two weeks, they were not fed for two days prior to the initiation of the experiment. Thus the fish experienced a period of “low prey availability.” Figure 2 shows the fish consumed more green shrimp during the

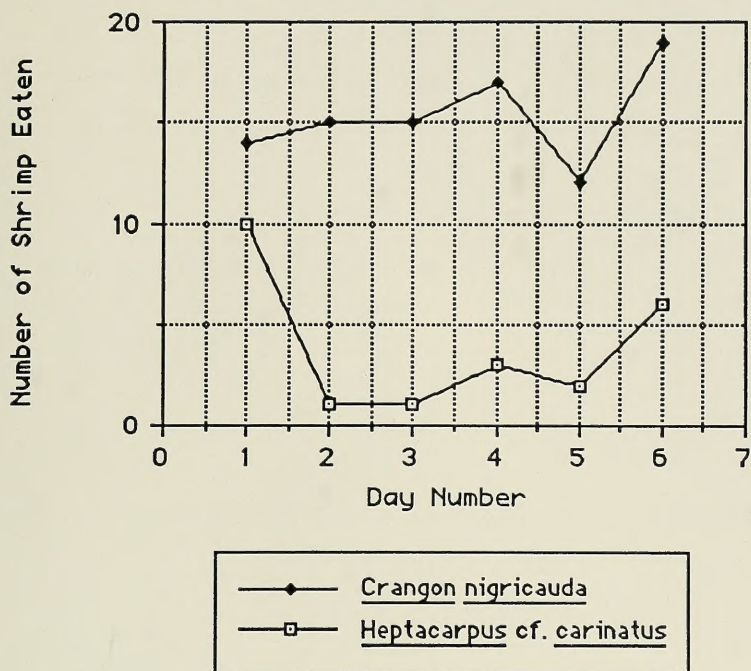


Fig. 2. The total number of *Heptacarpus cf. carinatus* and *Crangon nigricauda* eaten by both *Leptocottus armatus* and *Scorpaenichthys marmoratus* as a function of time. The sculpins were not fed two days prior to experimentation.

first 12-hour period than at any other time. This extremely limited information does suggest the possibility that the fish might prey arbitrarily when food availability is low. As they became well fed ("high prey availability") a significant preference developed. Further studies comparing prey choices in hungry fish versus well-fed fish are needed to address this hypothesis. Alternatively, the variety of prey organisms in the natural environment may be so diverse that a preference between two species is not discernible. An examination of cabezon stomach contents by Myers (1979) found over eight different, but unidentified, shrimp species consumed.

This form of quantitative analysis in sculpin food preferences is just the starting point for additional studies. Further exploration of fish prey preferences may eventually provide information relevant to movements in fish populations, nutritional information for fish farmers, as well as understanding the interactions of ecological communities as a whole.

Acknowledgments

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452-458.

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COVER: A monarch butterfly (*Danars plexippus*) drinking from dew-dampened vegetation near an overwintering site. (Page 1). Photo by P. H. Wells.